BELOWGROUND MERISTEM DENSITY OF WARM-SEASON GRASSES AS REGULATORS OF GRASSLAND INVASIBILITY

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Abstract: Recent studies suggest that perennial grasslands susceptibility to invasions (i.e. invasibility) by exotic plants may be related to the population of native grass belowground meristems (the "bud bank") in these plant communities. In perennial grasslands, the belowground bud bank plays a fundamental role in local plant population persistence, structure and dynamics; all important factors determining invasibility. Using greenhouse and multiple field sites, Konza Prairie Biological Station (KPBS) and Oklahoma State University – Range Research Station (OSU-RRS), the following hypotheses were tested: 1) Bud:tiller ratios decrease with decreasing bud banks; 2) Increases in bud bank size will lead to increases in grassland stability, thereby reducing invasibility; and 3) Grassland invasibility is regulated by a minimum threshold in bud bank densities. Treatment levels were created by establishing a 0%, 33%, 66%, and 100% bud bank gradient of natural field densities of *Schizachyrium scoparium* (greenhouse), and *Schizachyrium scoparium, Andropogon gerardii, Sorghastrum nutans,* and *Panicum virgatum* (field). Invasive species *Bothriochloa bladhii* at KPBS and *Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata* at OSU-RRS and greenhouse were sown in each plot and mesocosm at a rate of 300 seeds species^{-1} m^{-2}. At greenhouse and both field sites, the lowest meristem density (0%) substantially decreased stability and increased invasibility of my grassland community. No significant differences were observed in bud:tiller ratios between the various bud bank density plots at KPBS and OSU-RRS. KPBS and OSU-RRS 2-year average KPBS and OSU-RRS 2-year average, and greenhouse (1-year) aboveground exotic species biomass from plots and mesocosms absent of bud bank (0%) was 10,165%, 467% and 800% greater than the low (33%) bud bank density plots, respectively. However, no relationship was observed between the various bud bank densities (33%, 66%, or 100%) and invasibility of these grassland communities (field) and populations (greenhouse). At both sites and greenhouse, the exotic species biomass production was not proportional to the bud bank population, and suggests the existence of an invasibility threshold between 0 and 33% of the bud bank density. An important implication of these findings is that perennial grasslands that maintain large bud banks are most resistant to exotic species invasions.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

CHAPTER 2

CHAPTER 3

Table Page

LIST OF FIGURES

Figure Page

CHAPTER 2

CHAPTER 3

Figure Page

CHAPTER I

INTRODUCTION

Grasslands are the most extensive terrestrial biome, covering approximately 40% of the Earth's surface excluding Antarctica and Greenland (White et al. 2000; Anderson 2006). Grasslands and other biomes are affected by elements of global environmental change, with biological invasions constituting a significant component of this change. Recent studies in the North American grasslands have shown that the belowground meristem population or "bud bank", rather than seeds, is the primary source for plant recruitment and of much greater importance to plant population persistence and productivity (Benson et al. 2004; Benson and Hartnett 2006; Dalgleish and Hartnett 2006). Understanding and predicting how perennial grassland bud banks respond to environmental change has been increasingly emphasized (Smith and Knapp 2001; Benson et al. 2004; Dalgleish and Hartnett 2006; Dalgleish and Hartnett 2009; Dalgleish et al 2008).

Using a one-year greenhouse mesocosm study and a two-year multi-site field Study, my research assesses the potentially important role of bud banks in conferring

resistance to invasion by exotic species. In both greenhouse and field studies, invasibility (susceptibility to invasion) was assessed as the total aboveground biomass of all exotic species.

Chapter 2 is a description of my greenhouse study. In this study, I examine invasibility of bunchgrass dominated grasslands under controlled conditions. My representative grass, a dominant tallgrass prairie perennial warm-season caespitose grass, was *Schizachyrium scoparium* (little bluestem). My study assesses invasion using three ecologically and environmentally important exotic species, *Bothriochloa ischaemum* (yellow bluestem), *Bromus japonicus* (Japanese brome), and *Lespedeza cuneata* (sericea lespedeza). My first objective in Chapter 2 was to test if reducing bud bank size results in a loss of resistance to invasion by exotic species. If low bud bank size does increase invasibility, then my mesocosms containing smaller bud banks will have a significant increase in exotic species biomass compared to mesocosms with larger bud banks. My hypothesis is that grassland communities with large numbers of belowground buds have the potential to regulate exotic species invasions. My second objective in Chapter 2 was to test the hypothesis that the invasibility of my warm-season grass population is regulated by a minimum threshold in bud bank densities. I hypothesize that a minimum invasibility threshold will occur in grassland. I expect this threshold to exist between 50% or fewer of the native field density of warm-season grass belowground buds (highly compromised bud banks due to biotic or abiotic alterations) and systems with no belowground buds (for example, grassland systems following high levels of disturbance).

For Chapter 3, I further assess the role bud banks play in resisting invasion by exotic species by conducting a 2-year multi-site (Kansas and Oklahoma) field study. The vegetation

of both sites was dominated by the perennial warm-season grasses, *Schizachyrium scoparium* (little bluestem), *Andropogon gerardii* (big bluestem), *Sorghastrum nutans* (Indiangrass), and *Panicum virgatum* (switchgrass). Invasive species *Bothriochloa bladhii* was used at the Kansas site and, *Bothriochloa ischaemum* (yellow bluestem), *Bromus japonicus* (Japanese brome), and *Lespedeza cuneata* (sericea lespedeza) (the same exotic species used for the greenhouse study) were used at the Oklahoma site. The first objective in Chapter 3 was to determine the relationship between belowground buds and tiller number. To determine this relationship, I examined bud:tiller ratios by destructively harvesting experimentally established treatments of varying tiller densities and assessing both the number of buds present and total tillers present. I hypothesized that tiller initiation will increase in response to a reduction in belowground buds, thereby increasing bud:tiller ratio in treatments with a reduced number of buds compared to those with buds at field density. However, there may be a consistent allometric relationship between number of buds and tillers present, i.e. my hypothesis is not supported and buds initiate tillers in a consistent pattern regardless of bud density. If a consistent relationship exists and I find similar bud:tiller ratios for each of my established bud densities, this will allow for extrapolation from tiller assessments to belowground buds present. The second objective in Chapter 3 was to test whether increases in bud bank size leads to increases in grassland stability (resistance to change), thereby reducing invasibility. I hypothesize that increases in bud bank size strongly correlates with increases in grassland stability (decrease in invasibility). The final objective of Chapter 3 was to determine whether the invasibility of my warm-season grass community was regulated by a minimum threshold in bud bank densities. Similar to the greenhouse study, I suggests that a

minimum invasibility threshold would occur at a point between no warm-season grass belowground buds present and 33% availability of the field bud bank density.

My dissertation presents research that furthers the understanding of belowground meristem population dynamics and their role in patterns of plant community structure and stability. My research indicates that belowground bud banks play an important role in resistance to invasion by exotic species.

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CHAPTER II

BUD BANK DEMOGRAPHY: DENSITY OF NATIVE CAESPITOSE GRASS MERISTEMS AS A PREDICTOR OF RANGELAND INVASIBILITY

ABSTRACT

Recent studies indicate that the belowground bud bank (i.e. belowground meristem population), rather than the seed bank, is the primary source of new tiller recruitment in tallgrass prairie. Therefore, grassland susceptibility to invasion (i.e. invasibility) by exotic plants may be related to belowground bud bank densities. In my study, the following hypotheses were tested: 1) Reductions in bud bank size will lead to decreases in invasion resistance to exotic grasses, and 2) Grassland invasibility is regulated by a minimum threshold in native belowground meristem population or "bud bank" densities. Field-collected *Schizachyrium scoparium* meristems were transplanted into greenhouse 25 kg soil-containing mesocosms (20 X 42 X 32 cm) at 0% (control), 33%, 66%, and 100% natural field densities of belowground buds. After tiller emergence of *S. scoparium*, seeds of three exotic species, *Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata* were sown (300 viable seeds species^{-1} m^{-2}) into each mesocosm. The mesocosms were maintained in a 18 – 36^{o}C greenhouse for 18 weeks. Exotic species invasibility was assessed by quantifying exotic species biomass at the conclusion of the study. Biomass production of exotic species was profoundly increased (>800%) in mesocosms which did not receive *S. scoparium* buds compared to mesocosms with bud banks, regardless of the meristem density. Final biomass of the exotic species was 410.40 g, 45.21 g, 19.05 g, and 12.68 g for 0%, 33%, 66%, and 100% of field bud densities, respectively. Invasibility of my grassland plant population was associated with a minimum threshold (4,500 buds m^{-2}) in bud bank densities, as even the lowest density of *S. scoparium* buds substantially increased stability and decreased invasibility compared to mesocosms containing no *S. scoparium* buds. An important consequence of my research is that maintaining perennial grassland plant populations with large reserve bud banks may increase resistance to invasion by exotic species.

INTRODUCTION

Grasslands, savannas, and shrub steppe ecosystems comprise the greatest percentage of global land cover, occupying over 24 million km^2 worldwide (Leith, 1978; Janisova, 2006). Across several continents perennial grasslands are the most important ecosystems supporting human livelihoods and providing key ecosystem services. Understanding the processes influencing grassland plant communities and ecosystem structure and function is crucial to developing sound management strategies for their sustainable use and for predicting their response to global environmental changes such as exotic species invasion. In perennial grasslands, the belowground population of meristems, or 'bud bank' as coined by Harper (1977), plays a fundamental role in local plant population persistence, structure, and dynamics (Dalgleish and Hartnett 2006). Recent studies in the North American grasslands have shown that the bud bank, rather than seeds, is the primary source for plant recruitment and of much greater importance to plant population persistence and productivity (Benson et al. 2004; Benson and Hartnett 2006; Dalgleish and Hartnett 2006). Even in a heavily disturbed grassland site, belowground meristems made a significantly larger contribution to plant recruitment than did seed rain or seed bank (Rogers and Hartnett 2001). Moreover, unlike seed banks, the bud bank has been found to more closely resemble the aboveground plant community (Bensen et al. 2004, Dalgleish and Hartnett 2006). In these grassland ecosystems, the reserve bud bank has been shown to be an excellent predictor of long-term annual net primary productivity (ANPP), indicating that bud bank dynamics and resulting tiller densities, rather individual tiller growth, are the primary drivers in NPP. Recent studies have also found that ecosystem invasibility is inversely related to ANPP (Smith and

Knapp, 2001; Stephenson and van Mantgem, 2005; Davies, et al. 2007; Schoolmaster and Snyder, 2010). These studies, therefore, suggest that a simple quantification of bud bank densities may be an excellent predictor of resilience stability and resistance to invasive exotic species in grassland plant communities.

My study assesses the potentially important role of belowground bud banks in grassland ecosystems in conferring resistance to invasion. Belowground bud banks may allow native grass plant species to maintain a large reserve propagule pool, thereby reducing windows of opportunity for invasive species. However, grassland disturbances from management practices such as high grazing intensities, or abiotic changes such as drought, may compromise the native bud propagule pool with a resultant decrease in resistance to invasibility. Theoretically, perennial warm-season grasslands with high bud bank densities enable rapid reductions in the availability of unused resources in early spring. Greater resource availability may result in strong negative interactions with plants reproducing from seed, thereby reducing invasibility and rendering habitats more stable (ability to limit exotic species biomass production) (Fig. 1). I suggest the existence of a non-linear response in exotic species biomass production with a clear minimum threshold of the belowground bud density (i.e. buds m^{-2}) that prevents invasion by exotic species. Therefore I assessed whether the invasibility of a warm-season caespitose grass-dominated community was regulated by a minimum threshold of belowground bud bank densities, and if bud bank density could serve as a good predictor of grassland community invasibility (Fig. 1). Caespitose growth forms are abundant in many warm-season dominated grassland biomes. As a model native caespitose plant species for my study, I selected *Schizachrium scoparium* (little bluestem). Because bud bank densities

are expected to decrease in response to grassland disturbances (Dalgleish and Hartnett 2009), my overall objective was to assess if the density of native *S. scoparium* is a primary factor influencing invasion by exotic species. More specifically, the following hypotheses were assessed (1) reduction in bud bank size is associated with greater invasibility and lower temporal stability (resistant to change) or resilience of plant populations (Fig. 1); and (2) invasibility in grasslands is regulated by a minimum threshold in belowground meristem population (Fig. 1).

MATERIALS AND METHODS

Exotic Species Seed Collection and Germination Tests

At the end of the growing season in the year prior to the greenhouse experiment, seeds of the exotic grass species were collected from tallgrass prairie at the Oklahoma Range Research Station (OSU-RRS), and *Lespedeza cuneata* seeds were purchased from a certified seed company. Collected and purchased seeds were stored in a seed storage room with 5^{o}C constant temperature (cold stratified) and 30% relative humidity until germination tests. Germination tests were conducted during winter 2008/2009 to determine seed viability. Each test was conducted according to ISTA (2005) testing standards. Each test consisted of four hundred (400) seeds which were drawn from the seed lot and then randomly divided into eight (8) replicates of 50 seeds. Seeds for each replicate were place on moist blotter/filter paper and a layer of sterile, moist very fine sand (0.05 – 0.10 mm diameter) placed over the seeds in a 9 cm diameter transparent disposable Petri dish. Relative humidity was kept as close to saturation as possible to reduce watering. Seeds were misted with distilled water as necessary. Seeds were

considered germinated when either the root or shoot structure exceeded the length of the caryopsis. Germinated seedlings were removed at each daily census and test duration was 14 days. Germination was expressed as the percentage of seeds reaching germination.

Experimental set-up

Soil was collected from an annually burned lowland site at the Konza Prairie Biological Station (KPBS), Manhattan, KS. The soil, identified as a Benfield fine, mixed, superactive, mesic Udertic Argiustoll, was sieved through a 5 mm sieve to remove rhizomes, roots, and pebbles. Twenty-five kg of soil was placed into 20 mesocosms (20 x 42 x 32 cm plastic containers with small holes on the underside) and placed in a greenhouse at Oklahoma State University. Soil-intact meristems of *S. scoparium* were collected from an annually burned watershed at KPBS, transported to Oklahoma State University and maintained in a 2 ^{o}C cold room until experimental setup. At experimental set-up, the meristems were washed free of soil and randomly transplanted into mesocosms in tightly packed, caespitose distributions simulating typical bunchgrass rangeland communities. The mesocosms were arranged in a randomized complete block design, with five replicates per treatment. Four distinct levels were simulated by transplanting zero, four, eight, or 12 caespitose bunches into five replicate mesocosms. Therefore, my treatments consisted of 0%, 33% (low), 66% (medium), or 100% (field density) of native bud bank field densities, respectively. My field density estimates indicated *S. scoparium* bud banks to be 13,500 buds m^{-2}. Therefore, on a square meter basis, my field density mesocosms received 13,500 buds, my low density contained 4,500 buds, and 9,000 buds were established into the medium density mesocosms.

After *S. scoparium* tiller emergence, seeds of three ecologically and economically important exotic species of the tallgrass prairie were sown in each mesocosm at 300 viable seeds species^{-1} m^{-2}. The three exotic species included a perennial C_4 warm-season caespitose grass (*Bothriochloa ischaemum:* yellow bluestem), an annual C_3 cool-season grass (*Bromus japonicus:* Japanese brome), and a perennial forb/sub-shrub (*Lespedeza cuneata*: Sericea lespedeza). Mesocosms were maintained on a diurnal 18 - 36 ^{o}C temperature regime to maximize growth of the warm-season grass selected for this study and watered periodically to field capacity throughout the experiment. Using weekly census throughout the 2009 growing season, invasibility of each of the mesocosms was assessed by quantifying the emergence, establishment, and survivorship of each exotic species. Native species were assessed monthly. At the end of the growing season (fall 2009), aboveground biomass was clipped at the soil surface, sorted by species, oven-dried at 60 ^{o}C for 48 hours, and weighed to the nearest 0.01g. The following definitions were applied for determining exotic species performance. Emergence was defined as the number of seedlings germinated but not exceeding 2 cm in height. Establishment was defined as the number of tillers or stems per mesocosm. Survival was defined as the proportion (%) of plants recorded at the 1st or 2nd census that were still present at the final census. Biomass was defined as the aboveground dry weight (g). Invasibility of each of the mesocosms was assessed as the total aboveground biomass of all exotic species. Exotic species performance (i.e. emergence, establishment, survivorship, and total biomass production), and tiller density were calculated.

Data Analysis

Exotic species performance was analyzed via one-way ANOVA (SAS 2007). Values are reported as means ± 1 SE, and were considered significant for all statistical tests at $\alpha < 0.05$ level. Duncan's multiple range test (square mass) was used to assure no existence of a Type I comparison-wise error rate. A Tukey's Studentized Range (HSD) Test (square mass) and Bonferroni (Dunn) t-Tests (square mass) were used to assure no existence of a Type I experiment-wise error rate.

RESULTS

Bud bank density comparisons to exotic species performance (invasibility)

Emergence: No relationship was observed between the bud bank densities and total exotic species as approximately 20% of all exotic seeds germinated in each of the mesocosms. Emergence success values for each exotic species are presented in (Fig. 2. A). There were no significant differences between an exotic species emergence in the 33% (low), (66%) medium, or (100%) belowground bud density mesocosms (Fig. 3. A).

Establishment: Total exotic species establishment was between 81.1 and 91.6 % for all treatment levels. Therefore, no relationship was observed between bud densities and exotic species establishment (Fig. 2. B). There were no significant differences between an exotic species establishment in the 33% (low), 66% (medium), or 100% belowground bud density mesocosms (Fig. 3. B).

Survivorship: Total exotic species survivorship was high, with nearly 100% established seedlings surviving throughout the study. Therefore, no relationship was observed between bud densities and exotic species survivorship (Fig. 2. C). There were

no significant differences between an exotic species survivorship in the 33% (low), 66% (medium), or 100% belowground bud density mesocosms (Fig. 3. C).

Aboveground Biomass: Total exotic species aboveground biomass was as much as 800% greater in the control (no *S. scoparium*) mesocosms, as compared to any mesocosm that contained *S. scoparium* buds, regardless of bud density. However, there were no significant differences between exotic species biomass production in the low, medium, or natural field density mesocosms (Fig. 2. D; Table 1). Likewise, no significant differences were observed between native *S. scoparium* production in the low, medium, or natural field density mesocosms. However, *S. scoparium* biomass production was profoundly increased in all mesocosms which received *S. scoparium* buds compared to mesocosms which did not receive *S. scoparium* buds (Fig. 2. F). Assessing aboveground biomass (or invasibility) of each exotic species individually indicates that not all exotic plants equally contributed to the overall biomass. In my study, the exotic warm-season grass, *B. ischaemum* was the largest contributor to overall exotic biomass production in the high disturbance (*S. scoparium* absent) mesocosms (Fig. 3. D). *Lespedeza cuneata*, the exotic forb/sub-shrub, produced significantly greater aboveground biomass in the high disturbance mesocosms (0% bud density) compared to low, medium or natural (100%) field density bud bank mesocosms. However, when the total exotic biomass of all three species was combined, *L. cuneata* contributed substantially less to the overall biomass than that observed by *B. ischaemum*. The exotic species *B. japonicus*, a cool-season grass, produced little biomass and did not contribute substantially to the total biomass production of any mesocosm (Fig. 3. D). However, *B. japonicus* survival and

establishment was high across all treatment levels, and had the greatest density (tillers m^{-2}) for the low field density bud bank mesocosms (Fig. 3.B, C, and E).

Density: At the end of the study, there were no significant differences in exotic species density (stems or tillers m^{-2}) between the 0, 33, 66, and 100% belowground bud density mesocosms (Fig. 2. E). Further, exotic species density was not attributed to a single species (Fig. 3. E; Fig. 4). *Lespedeza cuneata* density increased as bud bank density increased and strongly dominated the exotic species assemblage in the 66% and 100% belowground bud density mesocosms (Fig. 3. E; Fig. 4. C and D).

DISCUSSION

This study addressed the effects of *S. scoparium* belowground meristem density on invasibility as a measure of emergence, establishment, survivorship, and aboveground biomass of exotic species. Using a highly-clumped spatial distribution of belowground meristems, I examined (1) whether larger bud bank densities will be more invasion-resistant than smaller meristem densities, and (2) whether the invasibility of *S. scoparium* plant community is regulated by a minimum threshold in bud bank densities. Although previous research studying habitat invasibility have used richness or density of exotic species (Lonsdale 1999; Davies et al. 2005), what is most often ecologically and economically important is the exotic species biomass rather than richness or density (Guo 2008). However, it is important to note that biomass alone does not indicate the potential for currently noninvasive exotics to become invasive through evolutionary or future habitat changes (Taylor and Hastings 2005), and therefore, establishment, reproduction, survivorship, density, and size of the exotic species has been selected as the dependent variable when studying habitat invasibility (Lonsdale 1999; Davies et al. 2005). In my

study, I proposed that biomass best reflects invasibility, as plants must reach a minimum size class for reproductive success, resource acquisition, or sufficient inter-/intra-specific influence to have a negative ecological or economical impact.

Understanding and predicting how perennial grassland bud banks respond to environmental change has been increasingly emphasized (Smith and Knapp 2001; Benson et al. 2004; Dalgleish and Hartnett 2006; Dalgleish and Hartnett 2009; Dalgleish et al. 2008). Although not tested, recent observations have suggested that bud banks may have the potential to regulate exotic species invasions (Dalgleish and Hartnett 2009). Results from my study supported my first hypothesis that larger bud bank densities will be more invasion-resistant than smaller bud bank densities. Removal of all belowground buds profoundly increased exotic species biomass production, as compared to mesocosms that contained *S. scoparium* buds, regardless of bud bank density. At the species level, high disturbance greatly increased *B. ischaemum*, *B. japonicus*, and *L. cuneata* individual biomass production, as compared to biomass production in mesocosms that contained *S. scoparium*, regardless of bud bank density. However, there were no significant differences in total exotic species biomass production between mesocosms with 33%, 66%, or 100% field density belowground buds.

A species must pass through at least three main stages, introduction, colonization (where recruitment, establishment, survival, and reproduction must all occur), and spread before it will have an ecological and/or economic impact to be considered invasive. Although biomass was used for measuring invasibility in my study, other invasion performance measures (i.e. emergence, establishment, survivorship, and reproduction) within the second main stage (colonization), as well as density were measured to provide

further insight in the invasion process. Numerous factors may explain why no observable relationship was found for any of the invasion performance measures (emergence, establishment, survivorship, density, and biomass) across the meristem densities of my mesocosms (excluding the 0% control). The reasons may include, nurse-plant interactions, differences in resource patterns among different species, self-facilitation through modification of soil microbial communities, or soil nutrient availability leading to positive plant-soil feedbacks, or allelopathy. Knowing the roles of the different factors discussed here may improve predictive power regarding invasion resistance of native grassland communities.

Data from my study support the hypothesis that invasibility in grasslands is regulated by a minimum threshold in belowground meristem population densities. A non-linear relationship was observed when comparing total exotic species aboveground biomass across the bud bank density treatment levels. The minimum threshold was below the lowest (33%) native bud bank density or between 0 and 4,500 buds m^{-2}. At the species level, a similar non-linear relationship was observed when the individual exotic species, *B. ischaemum, B. japonicus,* and *L. cuneata* were compared across the treatment levels. Using rhizomatous tallgrass prairie warm-season grasses, Sprinkle (2010) conducted a similar study using the same temporal and spatial scales and the same exotic species as were used in my study, and reported a similar minimum threshold as I detected with caespitose grasses. Both of our studies found large increases in invasive species biomass between mesocosms with no belowground mersitems and mesocosms established with meristems at approximately 33% of field density. The minimum threshold found in my study indicated that none of the exotic species were able to achieve

the final step of invasion as described by Richardson and Pyšek (2006). Invasions of successionally mature, undisturbed communities (e.g. perennial grasslands) usually require that the exotic species overcome resistance posed by the following barriers, geographic, environmental (local), reproductive, dispersal, environmental (disturbed habitats), and the final barrier step (Richardson et al. 2000). Exotic species may overcome the early stages (e.g. emergence, establishment, survivorship), but if the final barrier is not met with success, then the species will not become invasive (Richardson and Pyšek 2006). As discussed earlier, biomass is clearly critical for assessing invasibility, especially in determining reproductive success and achieving the final state of invasion. For exotic species to be competitive with native species, they need time to buildup sufficient biomass to use space, light, water, nutrients, other resources, or to exert an influence (e.g. plant-soil feedback, allelopathy) on other species (Smith et al. 2004). Identifying thresholds will play a key role in understanding these barrier dynamics and predicting invasion resistance to exotic plant species by native grass communities. Predicting threshold disturbance levels before an ecosystem becomes susceptible to invasion is important since it can greatly assist prioritization decisions of invasive species management by targeting those species, and/or their particular invasion performance measures (e.g. emergence, establishment) most likely to successfully invade in disturbed grassland habitats.

The law of constant yield (Harper 1977) indicates that biomass and density are not always correlated, biomass can saturate or pervade even as density continues to increase, creating opportunities for biomass and density to have distinctly different influences on ecosystem functioning (Hulvey and Zavaleta 2012). Density alone may

serve as a measure of invasibility, but it is not as useful as biomass because the latter better reflects resource use (Guo and Rundel 1997). For example, one individual of a large-sized perennial exotic species may use far more resources than many individuals of a small annual species. However, if exotic species show a consistent pattern of tiller or stem density, there can be great strength in assessing trends in increases in biomass versus tiller density. For example, in a trend analysis where an exotic species is assessed individually there may be no evidence of increase in biomass, while density (i.e. number of tillers or stems m^{-2}) may increase. Alternatively, invasibility (or biomass production) may be highly significant when biomass is measured with no increase in density. Using both biomass and density can provide insights on the size of the exotic species, which has been another common invasion performance measure. For example, the relative increase in total exotic species biomass, (e.g. 0% bud bank density mesocosms) (Fig. 2 D), compared to total exotic species density for the same treatment (Fig. 2. E), reveals that there has been an increase in the average plant size with no corresponding increase in density (Fig. 3 D). At the species level, exotic species plant size is revealed when an individual exotic species biomass is small relative to its density. For example, at the end of the growing season, most *L. cuneata* stems were just exceeding emergence height (personal observation) and had very low biomass relative to its density (Fig. 3 D and E). Therefore, it important to note that selecting biomass as my exotic species performance indicator is context dependent; biomass depended on what species were considered. In my study, exotic species biomass throughout the study was driven by *B. ischaemum* (Fig. 3. D), while density at the end of the 18 week study was dominated by *L. cuneata* (Fig. 3. E).

Therefore, it may be argued that density be the performance indicator to assess invasion success. However, using density as an invasion performance measure, removal of all belowground buds did not significantly increase overall exotic species density, as compared to mesocosms that contained *S. scoparium* buds, regardless of bud bank density (Fig. 2.E). I did not observe any relationship between total or individual exotic species density and the bud bank densities, suggesting the absence of an invasibility threshold using density as a performance measure.

However, results of the study indicated that using density as the exotic species performance indicator is also context dependent. For example, density in the 66 and 100% bud density mesocosms was driven by *L. cuneata* (Fig. 3. E), but this was not evident at the other densities. Interestingly, *B. japonicus* had the highest density at the 33% native meristem density level, perhaps due to the right combination of adequate density of natives for nurse-plant effect and adequate light from less competition for space. Specifically, the native plants may have served as plants facilitating growth and development of other plant species beneath their canopy, thereby offering a benign microhabitat that is more favorable for seed germination and/or seedling growth, as well as avoiding herbivory. There was a general decrease in *B. ischaemum* density along an increasing bud bank gradient (Fig. 3. E), with a corresponding increase in *L. cuneata* density along these bud bank gradients. The dominance in density by *L. cuneata* at the end of the growing season may indicate this species is in an invasion lag phase, and possibly capable of rapid growth once favorable environmental conditions arise. Such a scenario, however, doesn't preclude *B. ischaemum* and *B. japonicus* being in an invasion lag phase as well.

Results of my study should add empirical support that restoring and maintaining large belowground meristem populations may aid land managers in regulating and limiting exotic plant invasions. Further, discovery of consistent non-linear responses in aboveground exotic species biomass with clear minimum thresholds may assist land managers in (1) anticipating and understanding ecosystem behavior when evaluating perennial grasslands, and (2) prioritizing management and restoration efforts. With that said, ANPP may need other performance measures (e.g. density) for predicting invasibility, especially if an exotic species is capable of persisting in communities with high bud bank densities until conditions become more favorable for its growth. An important consequence of my research is that a perennial grassland plant population with a large reserve bud bank may be most resistant to invasion by exotic species. The findings gained in this research begin a critical step in obtaining a better understanding of belowground bud banks in rangeland responses to invasion by exotic species.

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TABLES

Table 1. Measures of exotic species (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) success following seeding into microcosms of *Schizachyrum scoparium* belowground meristems established at 0%, 33%, 66% and 100% native *Schizachyrum scoparium* belowground meristem field density. (n=20; ± 1 Standard Error)

Treatment	**Measures of Exotic Species Success**				**Native**
Native Belowground Meristem Density (%)	Emergence (% seed)*	Establishment (% emergence)*	Survivorship (% survival) *	Aboveground Biomass ($g\ m^{-2}$) *	Native Aboveground Biomass ($g\ m^{-2}$)
0	19.5 ± 4.9[a]	91.6 ± 2.8 [a]	99.7 ± 3.0 [a]	410.4 ± 66.1 [a]	-
33	19.2 ± 1.6 [b]	85.7 ± 2.5 [b]	100 ± 0.5 [b]	45.2 ± 14.4 [b]	295.4 ± 169.2
66	21.8 ± 1.6 [b]	81.1 ± 3.9 [b]	88.4 ± 2.1 [b]	19.1 ± 5.5 [b]	384.6 ± 135.6
100	20.8 ± 2.1 [b]	88.3 ± 2.2 [b]	94.2 ± 3.1 [b]	12.7 ±3.5 [b]	372.0 ± 117.9
p-value	>0.05	>0.05	>0.05	0.0006	-

[a] = means within columns followed by the same letter are not statistically different (one-way ANOVA; $\alpha < 0.05$)

FIGURES

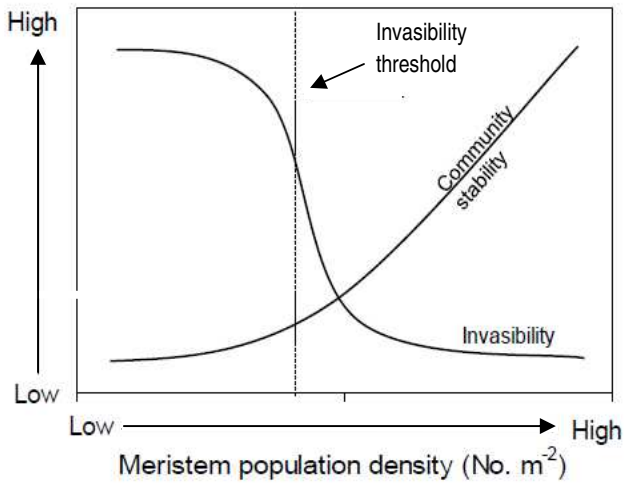
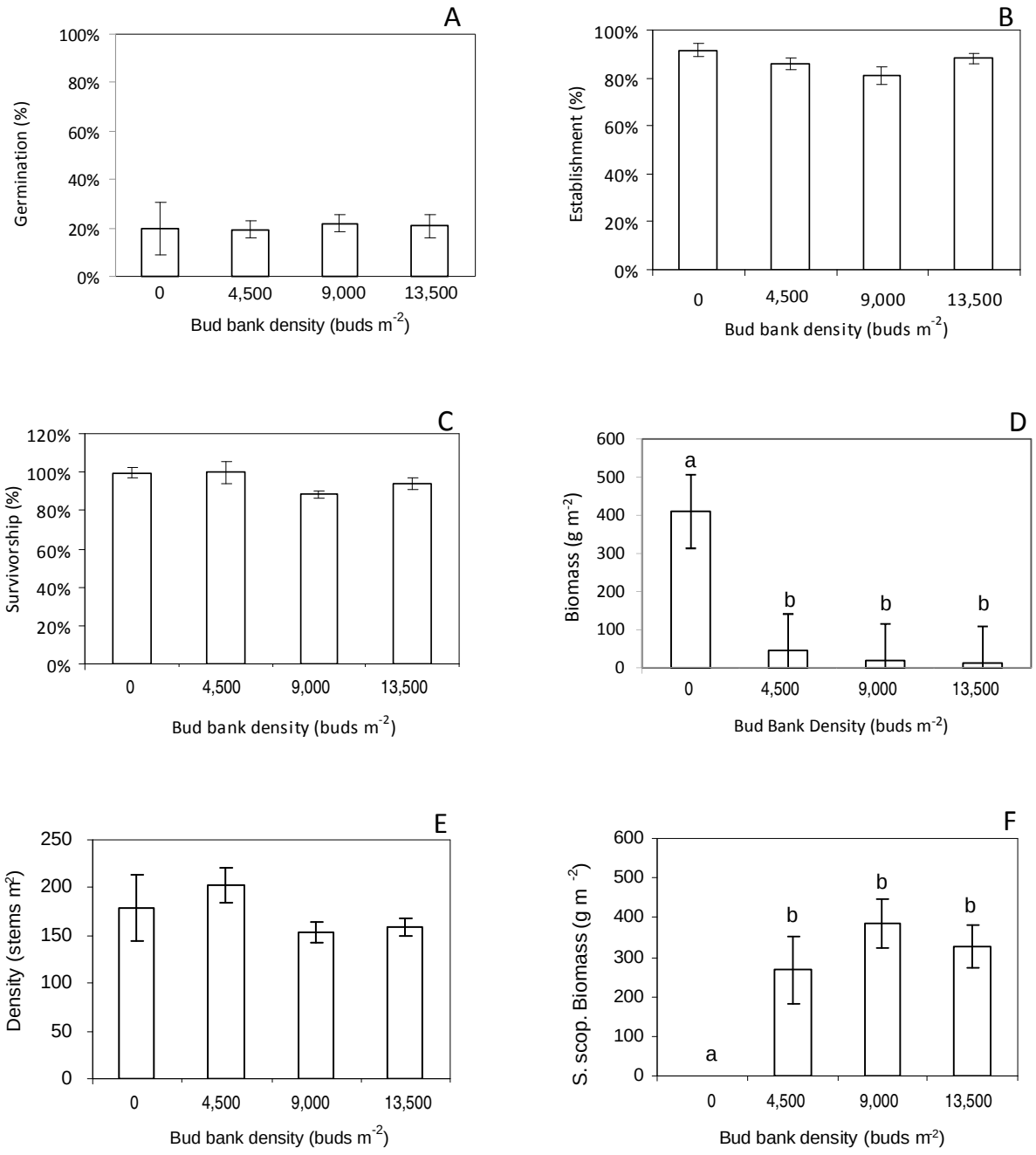


Figure 1.



*stems and tillers

Figure 2.

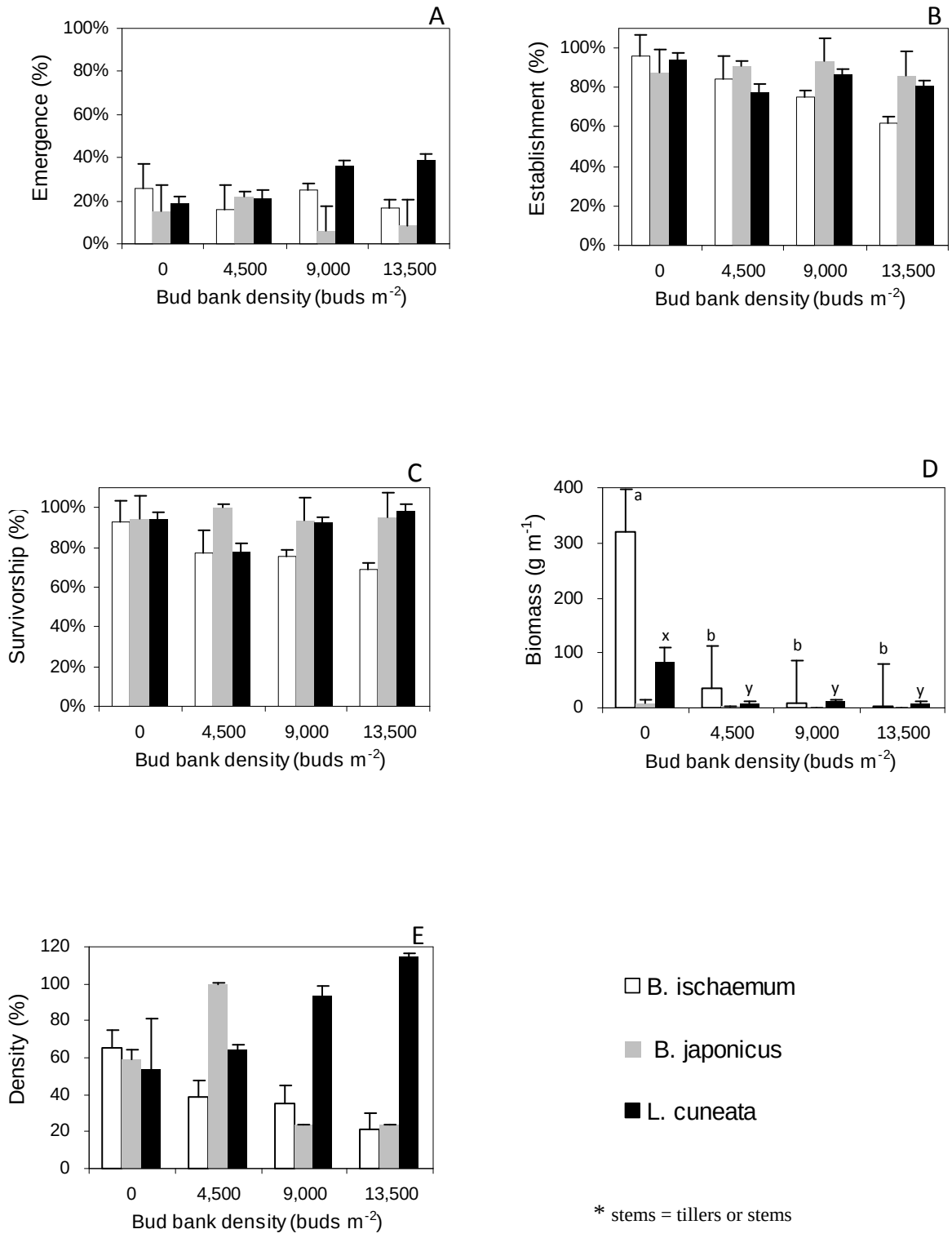
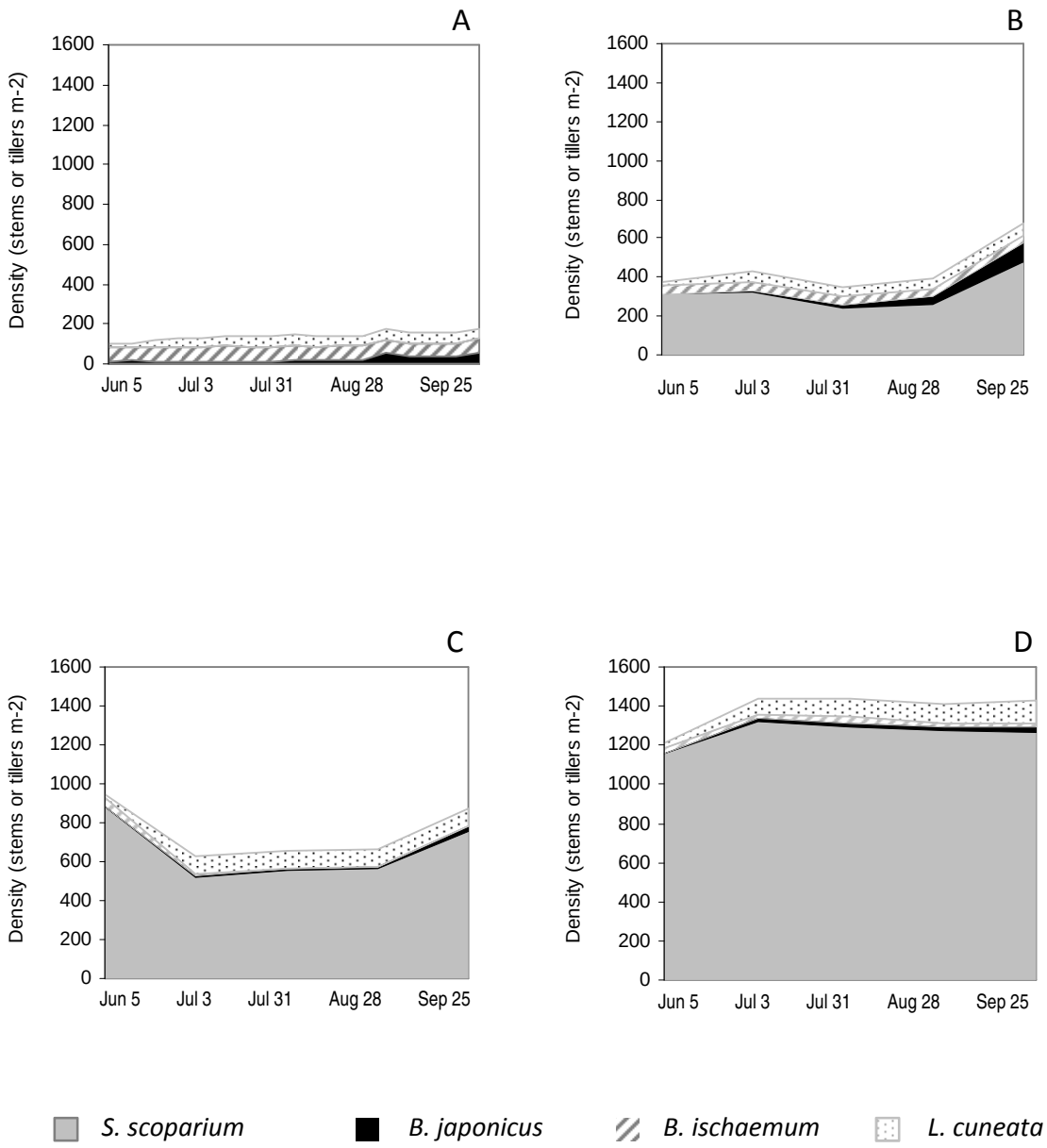

A
Emergence (%)
100%
80%
60%
40%
20%
0%
0
4,500
9,000
13,500
Bud bank density (buds m-2)
B
Establishment (%)
C
Survivorship (%)
D
Biomass (g m-1)
400
300
200
100
a
x
b
y
E
Density (%)
120
100
80
60
40
20
B. ischaemum
B. japonicus
L. cuneata
* stems = tillers or stems

Figure 3.



* Weekly sampling event dates not shown.

Figure 4.

FIGURE CAPTIONS

Figure 1. Hypothesized relationship between bud bank densities and native plant community invasibility and stability.

Figure 2. Emergence (A), establishment (B), survivorship (C), aboveground biomass (D) and density (E) of exotic species and *Schizachyrium scoparium* biomass (F) at 0 buds m^{-2} (0%), 4,500 buds m^{-2} (33%), 9,000 buds m^{-2} (66%), or 13,500 buds m^{-2} (100%) field (*Schizachyrium scoparium)* belowground bud densities. Significant ($\alpha < 0.05$) difference indicated by different letters above bars. Graphs with no significant difference among treatments have error bars ±SE.

Figure 3. Exotic (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) invasion performance measures, (A) emergence, (B), establishment, (C) survivorship, (D) biomass, and (E) density at 0 buds m^{-2} (0%), 4,500 buds m^{-2} (33%), 9,000 buds m^{-2} (66%), or 13,500 buds m^{-2} (100%) field (*Schizachyrium scoparium)* belowground bud densities. Bars with the same letter are not significantly different ($\alpha < 0.05$).

Figure 4. Tiller density of *Schizachyrium scoparium*, and exotic species *Bothriochloa ischaemum* and *Bromus japonicus*, and stem density of *Lespedeza cuneata* at of 0% (A), 33% (B), 66% (C), and 100% (D) native belowground bud densities of *Schizachyrium scoparium*.

CHAPTER III

BUD BANK DENSITY OF WARM-SEASON GRASSES AS REGULATORS OF GRASSLAND INVASIBILITY

ABSTRACT

Exotic species invasions have serious consequences for native species populations, biodiversity, and ecosystem processes. Thus, identifying factors that influence invasions by exotic plant species is of critical importance. In perennial grasslands, the belowground population of meristems or "bud bank" plays a fundamental role in local plant population persistence, structure and dynamics; all important factors determining invasibility. Using two field sites, Konza Prairie Biological Station (KPBS) and Oklahoma State University Range Research Station (OSU-RRS), the following hypotheses were tested:1) Decreases in native belowground buds promote tiller initiation, resulting in a decreased bud:tiller ratio; 2) Increases in bud bank size will lead to increases in grassland stability, thereby reducing invasibility; and 3) Grassland invasibility is regulated by a minimum threshold in bud bank densities. Treatment levels were established by thinning out native warm-season (C_4) grasses to create four different bud bank densities: control (0% or complete removal of belowground buds), low (33% of field bud density), medium (66% of field bud density), and field density (100% or no removal of belowground meristems). In the following two years, invasive species were sown in each plot at a rate of 300 viable seeds species^{-1} m^{-2}. *Bothriochloa bladhii* was selected for KPBS and *Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata* were selected for OSU-RRS, as these species are abundant at these sites. My results did not support the hypothesis that native belowground bud:tiller ratios decrease with decreasing bud bank size. At both sites, the control (total removal of all belowground meristems) substantially decreased stability and increased invasibility of our grassland community. KPBS and OSU 2-year average aboveground exotic species biomass from plots absent of belowground buds (control) was 10,165% and 467% greater than the low (33%) bud bank density plots, respectively. However, no relationship was observed between the 33%, 66%, or 100% field density treatments and invasibility of these grassland communities. At both sites, the exotic

species biomass production did not decrease proportionally with increased bud bank population. This suggests the existence of an invasibility threshold between total absence of belowground buds and 33% of field bud density. An important implication of these findings is that mesic perennial grasslands that maintain large bud banks are most resistant to exotic species invasions. These findings begin a critical step in obtaining a better understanding of the role of bud banks in rangeland responses to environmental change.

INTRODUCTION

Grasslands are the most extensive terrestrial biome, comprising one fifth of the Earth's land surface (NASA, 2012) and covering approximately 40% of the Earth's surface excluding Antarctica and Greenland (White et al. 2000; Anderson 2006). Grasslands are the center of the world's agricultural activities (Davis 2011) supporting human livelihoods and providing key ecosystem services. Grasslands and other biomes are affected by elements of global environmental change, with biological invasions constituting a significant component of this change. Environmental change (e.g. changing climate, changing fire regimes, alterations grazing managements, invasions of exotic plant species, nutrient enrichment) can result in a plethora of scenarios, such as shifts in plant composition leading to further biotic and abiotic changes in the environment (Jeltsch et al. 2011; Wellstein, et al. 2011). The response of perennial grasslands to environmental changes may be limited by belowground meristem or "bud bank" demography (Benson et al. 2004), since the bud bank is the primary source of plant regrowth (Benson et al. 2004; Benson and Hartnett 2006). For example, Benson and Hartnett (2004) found that regrowth of warm-season grasses of the tallgrass prairie occurs primarily (>99%) from vegetative recruits rather than recruitment from seed. In some grassland communities, bud bank dynamics may be a stronger driver of net primary

productivity than individual till growth size (Hartnett and Fay, 1998).

In perennial grasslands, maintenance of a bud bank incurs significant costs (Dalgleish 2007). The allocation of resources between belowground bud production and aboveground growth may be a bet-hedging strategy (Tuomi et al. 1994; Nilsson et al. 1996), whereby plants forgo growth opportunities in return for increased survival by avoiding unfavorable conditions. When conditions become favorable, recruitment from the bud bank enables rapid regrowth (Vesk and Westoby 2004, Benson et al. 2004) following soil disturbances (Rogers and Hartnett 2004), drought (Dalgleish and Hartnett 2006), fire (Dalgleish and Hartnett 2009), and herbivory (Ott and Hartnett 1011). Recent studies have investigated bud bank responses to disturbance events such as grazing and fire (Benson et al 2004; Benson and Hartnett 2006; Dalgleish and Hartnett 2009), nutrient limitation (Seastedt et al. 1991; Dalgleish and Hartnett 2008) and precipitation gradient (Dalgleish and Hartnett 2006). For example, in annually burned perennial prairie, the bud bank density at the onset of the growing season greatly exceeded aboveground tillers, suggesting that aboveground tiller populations are not meristem-limited (Benson et al. 2004). An important consequence is that perennial grasslands with high bud bank densities may be resistant to environmental change (e.g. exotic plant invasions). However, disturbances may influence invasibility (Burke and Grime 1996; Smith and Knapp 2001). Although several studies have investigated the effects of disturbance events and environmental conditions on bud bank demography, the association between different size belowground bud bank densities and tiller density has not been documented. Therefore, my first hypothesis is that bud per tiller ratio will decrease as bud bank densities decrease due to greater tiller initiation. This may be important as

increasing meristem limitation from disturbances may result in increased tiller initiation, possibly leading to alterations in plant community structure (Benson et al 2004; Dalgleish and Hartnett 2006; Dalgleish and Hartnett 2009).

Recent studies suggest that the bud bank of perennial grasses is a key characteristic influencing community structure, dynamics, and local population persistence (Dalgleish and Hartnett 2006); all important factors of how grassland plants respond to exotic plant species. Observations such as these suggest that grasslands susceptibility to invasion (i.e. invasibility) by exotic plants may be related to belowground bud bank densities in these plant communities (Hartnett 2009). However, this relationship has not been well tested.

Since invasion thresholds are a central concept underpinning restoration ecology (Hobbs and Harris 2001; Greenman and Pasour 2012), rangeland ecology (Walker 1993), and landscape or spatial ecology (Turner 2005), the practical implications are immense (Neri et al 2011). Surprisingly, identifying critical ecological thresholds in predicting invasibility, have scarcely been explored (Walker and Meyers 2004), yet these thresholds may be important for developing theories and models to anticipate invasibility in ecosystems (MEA 2005). I hypothesized that the bud bank-invasibility relationship for perennial grasslands is non-linear, with a minimum threshold of buds resulting in high invasibility. Therefore, greater temporal stability will be present in warm-season grassland communities with high bud bank densities.

My research assessed the following hypotheses: (1) bud:tiller ratios decrease with decreasing bud banks; (2) increases in belowground bud banks lead to increases in grassland stability (resistance to change), thereby reducing invasibility; and (3) grassland

plant community invasibility is regulated by a minimum threshold in belowground bud bank densities (Fig. 1). Using two tallgrass prairie field sites, my study addresses the theory that warm-season grass bud banks maintaining high densities will confer increase resistance to invasion by exotic species, resulting in grassland communities that are more stable than communities with lower bud bank densities.

MATERIALS AND METHODS

Exotic Species Seed Collection and Germination Tests

At the end of the growing season in 2009, the year prior to Year 1 (2010) and Year 2 (2011) field experiments, seeds of *Bothriochloa ischaemum* and *Bromus japonicus* were collected from tallgrass prairie at the Oklahoma Range Research Station (OSU-RRS), *Bothriochloa bladhii* seeds were collected the Konza Prairie Biological Station (KPBS), and *Lespedeza cuneata* seeds were purchased from a certified seed company. Seeds were stored in a seed storage room with 5^0C constant temperature (cold stratified) and 30% relative humidity until germination tests. Germination tests were conducted three times during winters of 2009/2010 and 2010/ 2011 to determine seed viability. Each test was conducted according to ISTA (2005) testing standards. Each test consisted of four hundred (400) seeds which were randomly drawn from the seed lot and then randomly divided into eight (8) replicates of 50 seeds. Seeds for each replicate were placed on moist blotter/filter paper and a layer of sterile, moist very fine sand (0.05 – 0.10 mm diameter) placed over the seeds in a 9 cm diameter transparent disposable Petri dish. Relative humidity was kept as close to saturation as possible to reduce watering. Seeds were misted with distilled water as necessary. Seeds were considered to be

germinated when either the root or shoot structure exceeded the length of the caryopsis. Germinated seedlings were removed at each daily census and test duration was 14 days. Germination was expressed as the percentage of seeds reaching germination.

Study area

Tallgrass prairie research sites located in Kansas and Oklahoma were used for this study. The Kansas site, Konza Prairie Biological Station (KPBS), a National Science Foundation (NSF) Long-Term Ecological Research (LTER) site, is located within the Flint Hills region of northeastern Kansas, 10 km south of Manhattan, Kansas, USA (39^{o}06'03.47"N, 96^{o} 36'36.8W) at an elevation of 350 m. Annual precipitation averages 835 mm. KPBS site soil type was a Clime, fine, mixed, active, mesic Udorthentic Haplustoll. The Clime series is a gently sloping and moderately deep, well-drained, silty clay loam with medium available water capacity and surface runoff (USDA-NRCS WSS 2012). The native vegetation is dominated by the perennial, warm-season grasses big bluestem (*Andropogon gerardii),* Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem *(Schizachyrium scoparium*). This site also has invasion by *B. bladhii*. The KPBS site was ungrazed and burned annually.

The Oklahoma site, Oklahoma State University Range Research Station (OSU-RRS) is located in the western part of the Cross Timbers ecosystem, 12.9 km southwest of Stillwater, Oklahoma, USA (36^{o}03'51.70"N, 97^{o} 13'47.08W) at an elevation of 326 m. Annual precipitation averages 932 mm. OSU-RRS soil type was a Coyle, fine-loamy, siliceous, active, thermic Udic Argiustoll. Natural organic content is high for this site (USDA-NRCS WSS 2012), which was last cultivated in the 1970's (Stansberry, 2010). The Coyle series is a gently sloping and moderately deep, well-drained clay loam with

medium available water capacity and surface runoff. The native vegetation is dominated by the perennial, warm-season grasses big bluestem (*Andropogon gerardii)*, Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem *(Schizachyrium scoparium*). This site also has invasion by *B. ischaemum, B. japonicus*, and *L. cuneata*. The OSU-RRS site was ungrazed and burned annually.

2010 and 2011 were below-average years for total precipitation at KPBS (2010: 598 mm, 28% below average; 2011: 753 mm, 10% below average). Warm seasonal precipitation was also below the long-term average (2010 Mar–Oct: 548 mm, 25% below average; 2011 Mar–Jul: 369 mm, 16% below average). 2010 and 2011 were below-average years for total precipitation at the OSU-RRS as well (2010: 812 mm, 13% below average; 2011: 585 mm, 37% below average). Warm seasonal precipitation was also below the long-term average (2010 Mar–Oct: 680 mm, 9% below average; 2011 Mar–Jul: 241mm, 50% below average). The seasonal precipitation (Mar–Jul) was 271 mm lower in 2011 than in 2010.

Native plant communities and invasive species

At both sites, the vegetation is dominated by perennial, warm-season grasses (i.e. *Andropogon gerardii, Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum virgatum*). Subdominant species include cool-season C_3 grasses (KPBS only), forbs, and a few woody species.

Study 1: Assessment of bud: tiller ratio

Experimental design and field setup

At both sites, corresponding (i.e. corresponding to the main 1 m^2 "invasion" field plots) field plots were established in early spring 2010 using (32) 0.125m^2 plots (in 4

blocks of 4 plots for each year of the two-year project) arranged in a randomized complete block design. Plots were separated by a distance of 2 m or greater to insure spatial independence with respect to soil and vegetation characteristics likely to influence local seedling or tiller establishment. Plots were metal-tagged for identification after annual burn, marked on all 4 corners of each plot with color-coded flags for treatment type, and their borders delineated with brightly-colored masonry cord for better visibility. Prior to treatment, percent cover of plant functional types (warm-season grasses, cool-season grasses, forbs, and woody species) was estimated using a modified (i.e. percent cover scale: 1 = < 1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%; 6 = 75-95%; and 7= > 95%) Daubenmire (1959) method.

Experimental establishment of belowground bud bank densities

In late spring 2010, native warm-season grasses were eliminated with glyphosate to experimentally establish: Control = 0% (elimination of all warm-season grasses), low (33% removal of warm-season grass tillers), medium (66% removal), and high (100% belowground bud field densities = no alteration in warm-season grass tiller density).

Field sampling

Throughout the 2010 and 2011 growing seasons, percent cover of C_3 and C_4 grasses, forbs and woody species was estimated. Tiller density was determined by quantifying the total tillers. At senescence, warm-season grasses were harvested by excavating to a 15-cm depth to ensure inclusion of all interconnected perennating organs (rhizomes and buds). Following harvest, plants were washed to remove soil.

Year-1 growing season: By fall at the KPBS site, the warm-season grasses had completed anthesis and some tillers had senesced. Flowering tillers were then counted.

By late September at the OSU-RRS site, the warm-season grasses had completed anthesis and flowering tillers were counted.

Year-2 growing season: By mid-summer, the warm-season grasses at the KPBS site had completed anthesis, and flowering tillers were counted. By late summer, the warm-season grasses at the OSU-RRS site had completed anthesis, and some tillers had senesced. Flowering tillers were then counted.

Laboratory methods and analysis

Belowground buds were examined using 7X and 10X magnification. Buds and flowering tillers were counted, assessed as living or dead, and categorized as live or dead buds. Live buds included developmental, mature, and activated buds. Dead buds were easily identified by their mealy or soft light-brown to dark-brown interiors. Flowering tillers were tillers with seed head entirely exposed. Laboratory tiller counts closely resembled field tiller census, and therefore, laboratory tiller counts were used when calculating bud:stem ratios.

Assessment of treatment establishment

Main 1m^2 invasion plots (Study 2):

Stem density of native warm-season grass and exotic species communities

KPBS warm-season grass community: In Week 14 (2010), the low (33%) and medium (66%) native warm-season grass tiller density levels (a surrogate multiplier for bud bank density) was equivalent to 38% and 66% of the field (100%) tiller density, respectively (Table 3)

OSU warm-season grass community: In Week 27, 2010, the 33% and 66% tiller density levels were equivalent to 25% and 64% of the 100% tiller density, respectively (Table 4).

The KPBS 2-year average end-of-season percent tiller density (a proxy for percent belowground bud density) was 38.5 and 60% for the 33 and 66% tiller field density treatments, respectively. The OSU 2-year average end-of-season percent tiller density was 32.5 and 74.5 % for the 33 and 66% tiller field density treatments, respectively.

Data analysis

To test for the effects of bud density on exotic species performance, biomass of each exotic species (measure of growth success or invasibility) was compared with the various bud densities via one-way ANOVA using SAS 2007. Values are reported as means ± 1 SE, and were considered significant for all statistical tests at $\alpha < 0.05$ level. Duncan's multiple range test (square mass) was used to assure no existence of a Type I comparison wise error rate. A Tukey's Studentized Range (HSD) Test (square mass) and Bonferroni (Dunn) t Tests (square mass) were used to assure no existence of a Type I experiment wise error rate.

Study 2: Assessment of bud density and grassland invasibility

Experimental design and field setup

At both sites, field plots were established in early spring 2009 using 20 $1m^2$ plots (in 4 blocks of 5 plots each) arranged in a randomized complete block design. Plots were separated by a distance of 2 m or greater to insure spatial independence with respect to soil and vegetation characteristics likely to influence local seedling or tiller

establishment. Plots were metal-tagged for identification after annual burn, marked on all 4 corners of each plot with color-coded flags for treatment type, and their borders delineated with brightly-colored masonry cord. Prior to treatment, percent cover of plant functional types (warm-season grasses, cool-season grasses, forbs, and woody species) was estimated using a modified Daubenmire (1959) method.

Establishment of belowground bud bank densities

One year prior to Year 1 growing season (late spring 2009), native warm-season grasses were eliminated with glyphosate to experimentally establish four belowground bud density treatments: Control = 0% (elimination of all warm-season grasses), low (33% native belowground bud field density), medium (66% native field bud density), and field density (100% belowground bud field densities: no alteration in warm-season grass tiller density). Elimination of tillers are expected to represent similar reductions in belowground buds, as Benson and others (2004) reported that the bud bank generally reflected aboveground patterns in species composition and grass tiller number in annually burned grasslands. In spring of 2010 and 2011 at the KPBS site, seeds of the exotic species *Bothriochloa bladhii* (Caucasian bluestem, a perennial C_4 caespitose grass) were sown in each plot (300 viable seeds m^{-2}). *Bothriochloa bladhii* was used because the KPBS site was characterized by the presence of only this invasive species. In spring of 2010 and 2011 at the OSU-RRS site, seeds of the exotic species *Bromus japonicus* (Japanese brome, an annual C_3 grass), *Bothriochloa ischaemum* (yellow bluestem, a perennial C_4 caespitose grass), and *Lespedeza cuneata* (sericea lespedeza, a wood/shrub legume) were sown in each plot (300 viable seeds $species^{-1}$ m^{-2}). These species were used because the OSU-RRS site was characterized by their presence. Therefore my treatments

consisted of experimentally modified bud bank densities with no warm-season grass buds (0%), low (33% field bud density), medium (66% field bud density), and field density (100% of native warm-season grass belowground buds, with all treatments receiving seeds of exotic species.

Aboveground tiller sampling

Throughout the 2010 and 2011 growing seasons, cover of each plant functional type was estimated. Invasibility (density) was determined by quantifying the total tillers or stems produced by each invasive species. Invasibility was also assessed by measuring aboveground biomass at plant senescence.

Year-1 growing season: At the KPBS site on April 24, 2010, *B. bladhii* seeds were sown into the treatment plots. Establishment of the exotic species was assessed monthly. By July 24, 2010, it was determined that no invasion occurred for any of the KPBS field observations and monthly assessments were concluded. At the OSU-RRS site on April 30, 2010, *B. japonicus, B. ischaemum,* and *L. cuneata* seeds were sown into the plots and density was assessed monthly. By October, the native warm-season grasses at the OSU-RRS site had completed anthesis, and some tillers had senesced, and monthly assessments were concluded.

Year-2 growing season: At the KPBS site on April 24, 2011 *B. bladhii* seeds were sown into all plots, and monthly assessments were initiated. At the OSU-RRS site on April 15, 2011, exotic species were seeded into plots and monthly density assessments were initiated. By late August 2011, the warm-season grasses at both sites had completed anthesis and some tillers had senesced, therefore, the monthly assessments were concluded. At the time of each exotic species senescence, aboveground biomass was

clipped at the soil surface, sorted by warm-season and cool-season grass species, forbs and woody species, tillers or stems were counted and clipped biomass was oven-dried at 60^{o}C for 48 hours. Biomass was weighed to the nearest 0.01g to determine total aboveground biomass production of each exotic species and each functional group (Abrams et al. 1986). Total aboveground biomass of all exotic species was used as an indicator of invasibility.

Data analysis

To test for the effects of bud density on exotic species performance, biomass of each exotic species (measure of growth success or invasibility) was compared with the various bud densities via one-way ANOVA using SAS 2007. Values are reported as means ± 1 SE, and were considered significant for all statistical tests at $\alpha < 0.05$ level. Duncan's multiple range test (square mass) was used to assure no existence of a Type I comparison wise error rate. A Tukey's Studentized Range (HSD) Test (square mass) and Bonferroni (Dunn) t Tests (square mass) were used to assure no existence of a Type I experiment wise error rate.

RESULTS

Using two field studies (Oklahoma and Kansas), the following hypotheses were tested: (1) bud:tiller ratios will decrease with decreasing bud banks; (2) Increases in bud bank size will lead to increases in grassland stability, thereby reducing invasibility; and 3) Grassland invasibility is regulated by a minimum threshold in belowground bud bank population densities.

Study 1: Estimation of bud bank density (bud:tiller ratio)

The ratio of native warm-season grass belowground buds to native warm-season aboveground tillers was assessed to test my first hypothesis that bud:tiller ratios will decrease with decreasing bud banks. At both KPBS and OSU, no significant differences were observed between bud:tiller ratios and the 0, 33, 66, and 100% belowground bud density treatments. KPBS 2-year average bud:tiller ratios were 1.42, 1.81, 1.73, and 1.67 for 0, 33, 66, and 100% of the belowground bud field densities, respectively (Fig. 2.A); an average of 1.66 buds per tiller. None of the bud:tiller ratios for the various belowground bud density treatments were significantly ($\alpha < 0.05$) different from one another. Therefore, total tiller number in my plots was related to that of belowground buds (generally 1 tiller = 1.66 buds). OSU-RRS 2-year average bud:tiller ratios were 1.00, 2.47, 3.99, and 1.26 for the 0, 33, 66, and 100% belowground bud field densities, respectively (Fig. 2.B); an average of 2.18 buds per tiller.

Study 2: Assessment of exotic species biomass, density, and grassland invasibility

Aboveground Biomass:

KPBS site (Kansas site): No invasion occurred during year 1 (2010) growing season, however, invasion (biomass production of the exotic species) did occur in Year 2. Exotic species biomass data supported by my second hypothesis that decreases in the belowground bud bank lead to decreased grassland stability (resistance to change), thereby increasing invasibility. Exotic species (*B. bladhii*) aboveground biomass was as much as 10,162% greater in the control (0% warm-season tillers remaining) plots as compared to plots that contained warm-season grasses, regardless of bud bank density. However, there were no significant differences between exotic species (*B. bladhii*)

biomass production in the low (33%), medium (66%), or field density (100% of warm-season tillers remaining) plots (Table 1; Fig. 3.A).

OSU-RRS site (Oklahoma site): Similar patterns in exotic species biomass production observed at KPBS field site occurred at the OSU-RRS site. The 2-year average exotic species (*B. ischaemum, B. japonicus, and L. cuneata*) aboveground biomass was as much as 467% greater in the control (no native warm-season grasses) plots as compared to any plots that comprised warm-season grasses, regardless of bud density. However, there were no significant differences between exotic species biomass production in the low (33%), medium (66%), or field density (100% of warm-season grass buds) plots (Table 2; Fig. 3.B). At the species level for this multi-exotic species site in Year 1, *B. ischaemum* dominated the exotic species community across all bud bank densities (Fig. 4.A). In Year 2, *L. cuneata* surpassed *B. ischaemum* in biomass production across all bud bank densities (Fig. 4.B).

Minimum invasibility threshold in perennial warm-season grass bud bank

KPBS site: No minimum invasibility threshold could be determined for Year 1 due to lack of invasion. Year 2 exotic species (*B. bladhii*) biomass from field plots indicate a non-linear response relationship between the various native bud bank densities and invasion success by *B. bladhii* (Fig. 3.A). The data also suggest there is an invasibility threshold between 33% of the belowground bud field density (approximately 671 buds m^{-2}) and total removal of the warm-season grass buds (Table 3). Therefore, KPBS data supports my third hypothesis that grassland plant community invasibility is regulated by a minimum threshold in belowground bud bank densities. Year 2 end-of-season exotic species (*B. bladhii*) density from my field plots indicate a similar non-linear

relationship between the various native bud bank densities and density success by *B. bladhii*. The data suggest there is a threshold between 0% and 33% of the belowground bud field density plots, where stability decreases (invasibility increases) and exotic species are successful in establishing and reproducing. Removal of all belowground buds profoundly increased exotic species density, as compared to plots that consisted of warm-season grass buds, regardless of belowground bud density. In 2011, *B. bladhii* tiller density trend (% change over 4 weeks) for the control (0%) native bud bank density treatment was +200 at Week 5, then an density trend (% change over 5 weeks) of +50.7 was evident by Week 10, and finally an density trend (% change over 4 weeks) of +6.7 occurred at Week 14. At the end of the 2011 growing season, tiller density of this invasive exotic was 111 tiller m^{-2} for plots that did not contain any warm-season grasses, versus only 3 tillers m^{-2} for plots with buds reduced to as much as 33% of the native bud bank density (Fig. 5. A and B). *Bothriochloa bladhii* was not observed in the 66% and 100% native bud bank density plots (Fig. 5.C and D).

OSU-RRS site: At the Oklahoma site, where multiple exotic species were used, a strikingly similar non-linear response and minimum invasibility threshold were found. Both 2010 and 2011 seasons experienced a non-linear response relationship between the exotic species aboveground biomass and bud bank densities. Data from both years, as well as the 2-year average, suggest an invasibility threshold between a belowground meristem level of less than 33% of field density (397 buds m^{-2}) and total removal of belowground buds (0% of field density) (Table 4; Fig. 3.B). Therefore, OSU data supports my third hypothesis that grassland plant community invasibility is regulated by

a minimum threshold in belowground bud bank densities. At the species level, a similar non-linear response occurred when comparing *L. cuneata* aboveground biomass across the native bud density treatment levels, and was coupled with an invasibility threshold between 0 and 33% of field density. Neither non-linear response relationship, nor an invasibility threshold was found when comparing *J. japonicus* aboveground biomass among the treatment levels (Fig. 4.A and B).

Similar to KPBS, removal of all belowground buds profoundly increased exotic species density, as compared to plots that contained warm-season grass buds, regardless of belowground bud density. At the species level, overall exotic species trend density was not driven by one species (Fig. 6 and 7). In 2010, stem density of the control (0% belowground bud field density) plots were dominated by *B. ischaemum* and *L. cuneata*, with a trend of increasing density observed throughout the season. At Week 18 the exotic species assemblage began to shift with *B. ischaemum* surpassing *L. cuneata* in dominance (Fig. 6.A). At the 33% field bud density treatment, *B. japonicus* dominated the exotic plant assemblage throughout its growth period (Fig. 6.B). From Week 4 through Week 25, *L. cuneata* had greater density than *B. ischaemun*, then by the final week (Week 27) both species had nearly equal density. The bud bank densities reduced to 66% field bud density had a nearly co-dominant exotic species assemblage of *L. cuneata and B. japonicus* (Fig. 6.C). Following *B. japonicus* senescence, *L. cuneata* dominated the density of the exotic communities. In 2010, at the 100% field bud density, *B. japonicus* dominated the exotic species community throughout its growth period as both *L. cuneata* and *B. ischaemum* had very low stem production. However, in both 2010 and 2011, stem

or tiller production was very low for all three exotic species in the field density (100%) treatment density levels were relatively low throughout the 2010 season (Fig. 6.D).

At the onset in 2011, the exotic species density in the control plots was entirely attributed to *L. cuneata*. Then, similar to the *B. ischaemum* density trend observed for the 2010 33% field bud density treatments, *B. ischaemum* began an increasing trend toward the same level as *L. cuneata*. By the final week, *B. ischaemum* slightly surpassed *L. cuneata* in density (Fig. 7.A). In the 33% field bud density treatments, unlike 2010, *L. cuneata* dominated the exotic species community during *B. japonicus* growth (Fig. 7.B). There was relatively low *B. japonicus* and *B. ischaemum* density throughout the 2011 season. The 66% field bud density treatments were dominated by *L. cuneata*, similar to 2010. (Fig. 7.C). The 100% field bud density plots had essentially only *L. cuneata* stems (Fig. 7.D).

DISCUSSION

This 2-year multi-site study examined (1) whether bud:tiller ratios decrease with decreasing bud banks; (2) whether decrease in belowground bud bank size (i.e. population) will lead to decreases in grassland stability (resistance to change), thereby increasing invasibility; and (3) whether grassland plant community invasibility is regulated by a minimum threshold in belowground bud bank densities.

Results of Study 1 did not support my first hypothesis that bud:tiller ratios decrease with decreasing bud banks. No significant differences in bud:tiller ratios were observed between the control (0% or complete removal of belowground buds) low (33% of field bud density), medium (66% field bud density) and field bud density (100% or no

removal of belowground meristems) plots. Bud:tiller ratios for both KPBS and OSU-RRS field (100%) bud density plots ratios were strikingly similar to earlier studies (Benson et al 2004; Dalgleish and Hartnett, 2009) and likely not meristem limited, with bud:tiller ratios of one (1) or greater for all belowground bud density plots (Table 5; Fig. 2). In fact, since my bud:tiller ratio assessment was based on late summer and early fall samples, I may have underestimated bud:tiller ratios that occurred in the following spring. Tallgrass prairies grasses make gradual and continual deposits to the bud bank until the following growing season (Dalgleish and Hartnett 2006). Therefore, it is likely that competition for resources (water, light, and nutrients) rather than meristem limitation resulted in tiller emergence and/or mortality rates (Vesk and Westoby 2004, Benson et al 2004). Winning such competitions may be attributed to the ability to re-sprout rapidly from a pool of dormant meristems, conferring some benefits to offset meristem production and maintenance cost (Vesk and Westoby, 2004), and perhaps the pre-emption of resources from potential exotic invaders, enabling a resident plant community more resistant to invasion.

Results of my study support my second hypothesis that decreases in the belowground bud bank lead to decreased grassland stability (resistance to change), thereby increasing invasibility. At both KPBS and OSU-RRS sites, removal of all belowground buds profoundly increased exotic species biomass production, as compared to plots that consisted of native warm-season grasses, regardless of belowground bud density. Analysis at the species level indicates that not all exotic plants equally contributed to the overall biomass. At the OSU-RRS site, plots absent of native warm-season grass belowground buds greatly increased *B. ischaemum* and *B. japonicus*

individual biomass production, as compared to biomass production in plots that comprised native warm-season grasses, regardless of belowground bud density. However, there were no significant differences in total or individual exotic species biomass production between treatments with any warm-season grass belowground buds. Sprinkle (2010) recently conducted a greenhouse mesocosm study to examine the relationship between bud bank density and grassland stability in rhizomatous-dominated warm-season grass communities. In this study, mesocosms that did not contain native belowground buds were profoundly greater in exotic species biomass production (successful growth), as compared to mesocosms that contained native rhizomatous warm-season grass buds, regardless of bud bank density. This greenhouse study agrees with my field study, in that maintaining bud banks reduces the susceptibility of the tallgrass plant community to invasion by exotic plants, imparting stability to these communities by significantly limiting exotic species growth and reproduction.

At the community level for the multi-exotic species field plots of the Oklahoma site, exotic species *L. cuneata* and *B. ischaemum* dominated the exotic species community biomass among the various bud bank densities. An interesting pattern was revealed regarding exotic species dominance, based on biomass production, at the Oklahoma site. At the end of the first year, *B. ischaemum* dominated the exotic species community across all bud bank densities. However, by the end of Year 2, *L. cuneata* surpassed *B. ischaemum* in biomass production. This shift in dominance may be due to, but not limited to, *L. cuneata's* extensive root system over tallgrass prairie grasses (Blair and Fleer 2002), release of more effective allelopathic chemicals by *L. cuneata*, effects of shading as *L. cuneata* began to outsize the less shade-tolerate grasses, or the nitrogen-

fixing ability of *L. cuneata* with a resultant alteration in soil nutrient availability. Year 2 total precipitation was 37% below average, and this may have placed *L. cuneata* at a competitive advantage having more extensive root system than the prairie grasses (Blair and Fleer 2002), allowing it to dominate by better surviving periodic droughts (Ohlenbusch and Bidwell, 2001). Also, since annually burned tallgrass prairie is chronically nitrogen-deprived (Eisel et al. 1989; Hobbs et al. 1991; Seastedt et al. 1991; Ojima et al. 1994), a competitive edge may have been shifted to the nitrogen-fixing legume, *L. cuneata*.

At both the Kansas and Oklahoma sites, similar relationships were found using density of the exotic species as a measure of success. As with biomass, removal of all belowground buds profoundly increased exotic species density, as compared to plots that contained warm-season grass buds, regardless of belowground bud density. Community dominance, measured as warm-season grass biomass production, appears to negatively affect density of exotic plant species (Smith and Knapp 1999). At the species level for the 2010 OSU-RRS plots, end-of-season exotic species (*B. ischaemum* and *L. cuneata*) density greatly increased in plots absent of warm-season grass buds. In 2011, the same relationship was observed for all three exotic species (*B. ischaemum, B. japonicus, and L. cuneata*) as well as the exotic species (*B. bladhii*) at the KPBS site. Hartnett and Fay (1998) found that most of the variation in aboveground net primary production (ANNP) in tallgrass prairie could be accounted for by differences in tiller densities rather than differences in tiller size. Perhaps the same principle supports stem and tiller density as an invasion performance measure in grasslands. Interestingly, the low (33% field bud density) and medium (66% field bud density) plots for both years at the Oklahoma site

showed a general decline in native warm-season grass density corresponding with a general increase in *L. cuneata* density. Also, the Old World bluestem species, *B. bladhii* and *B. ischaemum* at the Kansas and Oklahoma sites, respectively, displayed a robust positive tiller density trend for the control (0% native bud density) treatments, never decreasing at any sampling point during my study. Density could be an equally or more important factor than biomass production for predicting invasibility, especially if the exotic species is capable of persisting in communities with high bud bank densities until conditions become more favorable for its growth – in essence, within an invasion lag phase.

Results from my study support my third hypothesis that grassland plant community invasibility is regulated by a minimum threshold in belowground bud bank densities. At both KPBS and OSU-RRS sites, the exotic species biomass production was not proportional to the belowground meristem population, and suggests the existence of an invasibility threshold between 0 and 33% of the belowground bud bank density. A recent greenhouse study using native rhizomatous grass plant communities and exotic species suggested an invasibility threshold occurred between 0 and 30% (800 tillers m^{-2}) of the estimated belowground bud density at KPBS (Sprinkle 2010). Native belowground meristems of my treatments with greater than 33% field bud density were sufficiently high enough to initiate new tiller growth. New tillers of the native grasses presumably were able to rapidly capitalize available resources such as water, light, and nutrients. Therefore, a threshold was observed, where fewer than 33% of field bud bank density was necessary for invasion by the exotic species to be successful.

At the species level for the multi-exotic species site (OSU-RRS), *B. ischaemum* and *L. cuneata* aboveground biomass each displayed a similar non-linear response as was observed at the Kansas site. Furthermore, this was accompanied by a minimum invasibility threshold between the control and 33% of the field bud bank density for both years: also similar to the KPBS site. However, *B. japonicus* did not display a non-linear response, and therefore, did not exhibit a minimum invasibility threshold. The importance of thresholds for land management has made them of critical importance in restoration (Hobbs and Harris 2001). Knowing the processes associated with these invasibility thresholds can assist land managers to anticipate and understand ecosystem behaviors when evaluating perennial grasslands (Tongway 2004). Further, thresholds can be used to prioritize management and restoration efforts (Bestelmeyer 2006). For example, already-crossed-threshold areas may be unlikely to respond to restoration actions, thereby would be considered low priority. Hence, consideration of thresholds provides a sorely needed prioritizing element to public and private lands management (Hobbs and Kristjanson 2003). The discovery of consistent thresholds in this study was intriguing and may aid in understanding non-linear exotic species response in perennial grasslands.

The relationships elucidated from this study emphasize the important role bud banks play in rangeland ecosystems in conferring resistance to invasion by maintaining high bud bank densities. Results of this study strongly support the suggestion that perennial grasslands with a large bud bank are most resistant to exotic species invasions. My findings begin a critical step in obtaining a better understanding of belowground bud banks in rangeland responses to environmental change.

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TABLES

Table 1. Measures of exotic species (*Bothriochloa bladhii*) success following seeding into 1m^2 plots of warm-season tallgrass prairie grass belowground meristems (n=16 ± SE) established at 0%, 33%, 66% and 100% native field bud density at Konza Prairie Biological Station (KPBS), 2010 and 2011 growing seasons.

Treatment	**Exotic Species Success (YR 1)**	**Native Species (YR 1)**	**Exotic Species Success (YR 2)**	**Native Species (YR 2)**	**Exotic Species Success (2-YR avg)**	**Native Species (2-YR avg)**
Native Belowground Meristem Density (%)	Aboveground Biomass (g m^{-2})	Native Aboveground Biomass (g m^{-2})	Aboveground Biomass (g m^{-2})	Native Aboveground Biomass (g m^{-2})	Aboveground Biomass (g m^{-2})	Native Aboveground Biomass (g m^{-2})
0	No invasion	3.69 ± 2.67	34.89 ± 15.27[a]	40.52 ± 16.73	17.45 ± 7.63 [a]	34.51 ± 15.76
33	No invasion	99.48 ± 16.82	0.34 ± 0.34[b]	176.26± 35.13	0.17± 0.17 [b]	171.26± 35.13
66	No invasion	260.46 ± 49.89	0.00 ±0.00 [b]	301.10 ± 13.56	0.00±0.00 [b]	301.10 ± 13.56
100	No invasion	3,777.98 ± 16.75	0.00±0.00[b]	366.68 ± 17.55	0.00 ± 0.00 [b]	366.68 ± 17.55
p-value	-	-	0.0001	-	0.0001	-

[a] = means within columns followed by the same letter are not statistically different (one-way ANOVA; α = 0.05)

Table 2. Measures of exotic (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) success following seeding into $1m^2$ plots of warm-season tallgrass prairie grass meristems (n=16; ± SE) established at 0%, 33%, 66% and 100% native field bud density at Oklahoma State University – Range Research Station (OSU-RRS), 2010 and 2011 growing seasons.

Treatment	**Exotic Species Success (YR 1)**	**Native Species (YR 1)**	**Exotic Species Success (YR 2)**	**Native Species (YR 2)**	**Exotic Species Success (2-YR avg)**	**Native Species (2-YR avg)**
Native Belowground Meristem Density (%)	Aboveground Biomass ($g\ m^{-2}$)	Native Aboveground Biomass ($g\ m^{-2}$)	Aboveground Biomass ($g\ m^{-2}$)	Native Aboveground Biomass ($g\ m^{-2}$)	Aboveground Biomass ($g\ m^{-2}$)	Native Aboveground Biomass ($g\ m^{-2}$)
0	149.58 ± 64.81[a]	0.00 ± 0.00	133.00 ± 36.25[a]	16.69 ± 13.22	117.14 ± 27.94 [a]	8.35 ± 6.61
33	22.21 ± 13.97 [b]	87.00 ± 53.74	14.21 ± 3.64 [b]	119.73 ± 39.04	18.21 ± 7.58 [b]	70.96 ± 26.98
66	7.25 ± 3.15 [b]	464.33 ± 47.84	3.08 ± 1.39 [b]	243.14 ± 38.68	5.16 ± 1.99 [b]	360.96 ± 11.12
100	2.52 ± 2.52 [b]	1,601.50 ± 318.55	0.95 ± 0.55 [b]	380.00 ± 69.65	1.73 ± 1.44 [b]	955.31± 161.6
p-value	-	-	0.0001	-	0.0001	-

[a] Superscripts indicate statistical similarity with columns (one-way ANOVA; $\alpha = 0.05$)

Table 3. Konza Prairie Biological Station (KPBS) native warm-season grass community tiller density (mean ± SE) and respective percent tiller density relative to the average 100% tiller density per sampling event among 0%, 33%, 66%, and 100% native field bud densities, for 2010 and 2011 growing seasons.

Sampling Event		Treatment (Percent Native Warm-Season Grass Bud Bank)			
2010		0%	33%	66%	100%
Week 14 (Jul 24)	Tillers m^{-2}	0.00 ± 0.00	375 ± 20	590 ± 60	995 ± 97
	Percent of 100%	0%	38%	59%	100%
2011		0%	33%	66%	100%
Week 13 (Jul 23)	Tillers m^{-2}	128 ± 38	404 ± 114	699 ± 71	1,033 ± 105
	Percent of 100%	12%	39%	68%	100%

Table 4. Oklahoma State University – Range Research Station (OSU-RRS) native warm-season grass community tiller density (mean ± SE) and respective percent tiller density relative to the average 100% tiller density per sampling event among 0%, 33%, 66%, and 100% native field bud densities, for 2010 and 2011 growing seasons.

Sampling Event		Treatment (Percent Native Warm-Season Grass Bud Bank)			
2010		0%	33%	66%	100%
Week 27 (Oct 30)	Tillers m^{-2}	0.00 ± 0.00	136 ± 28	351 ± 34	546 ± 168
	Percent of 100%	0%	25%	64%	100%
2011		0%	33%	66%	100%
Week 15	Tillers m^{-2}	80 ± 0.00	228 ± 9	509 ± 48	597 ± 87

Table 5. Konza Prairie Biological Station (KPBS),Oklahoma State University – Range Research Station (OSU-RRS), and cited literature bud and tiller densities and meristem limitation index values based on 100% native belowground bud density.

Site	Peak Bud Density* (buds m^{-2})	Peak Tiller Density* (stems m^{-2})	Meristem Limitation Index (total buds/total tillers**)
KPBS (2-YR† Average)	1901	1137	1.66
OSU (2-YR† Average)	1353	3023	2.18
KPBS (Dalgleish & Hartnett 2009)	2450 ± 231	1831 ± 167	1.35
KPBS) Benson et al. 2004)	1830 ± 330	-- --	
1997	-- --	1369 ± 158	1.3
1998			

* Estimates are means ± one standard error

** Tillers = flowering tillers

† 2010 and 2011

FIGURES

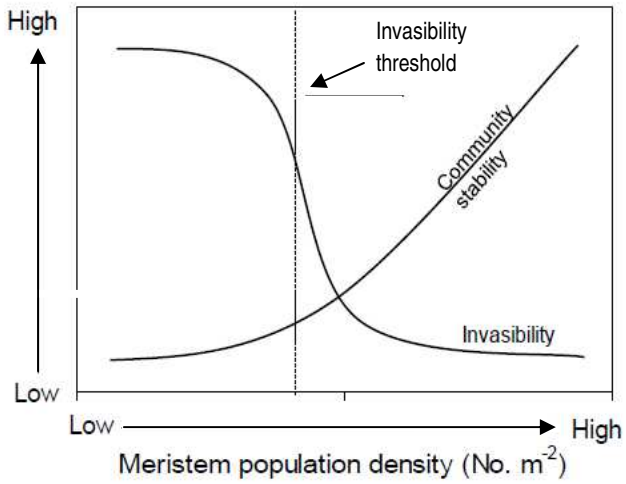
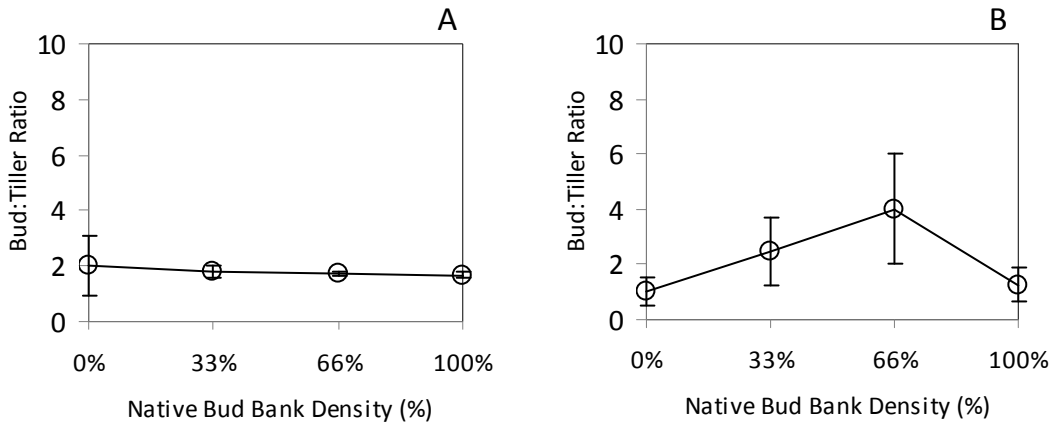


Figure 1.



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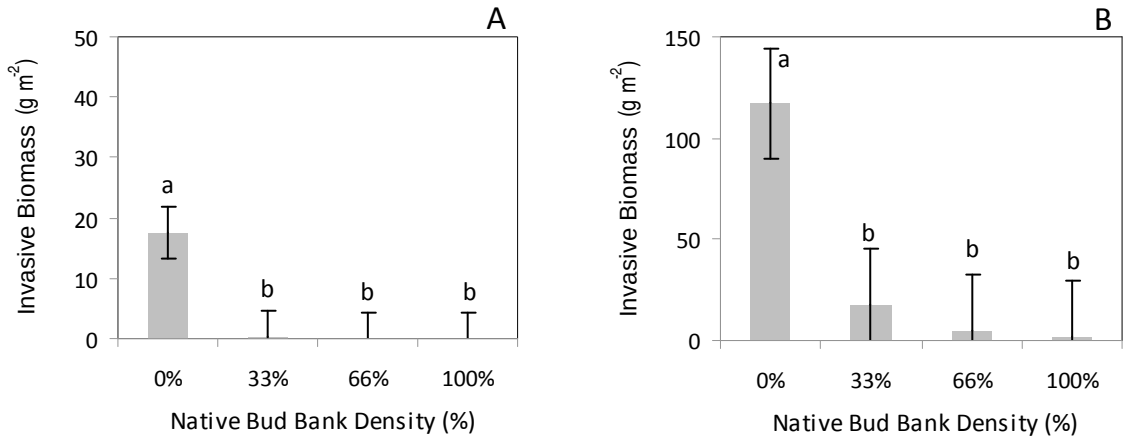

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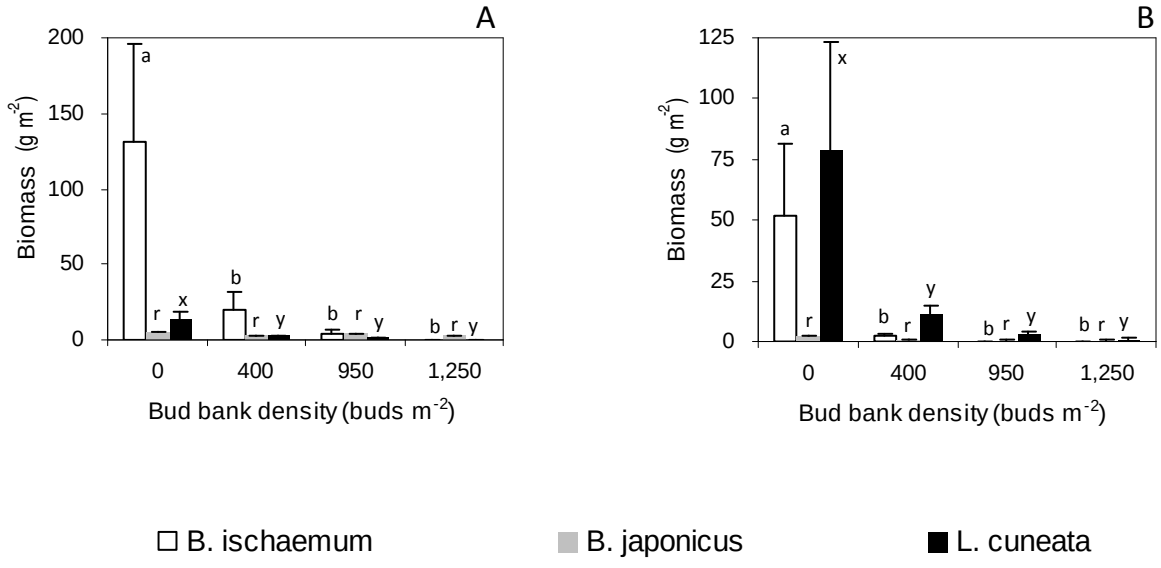

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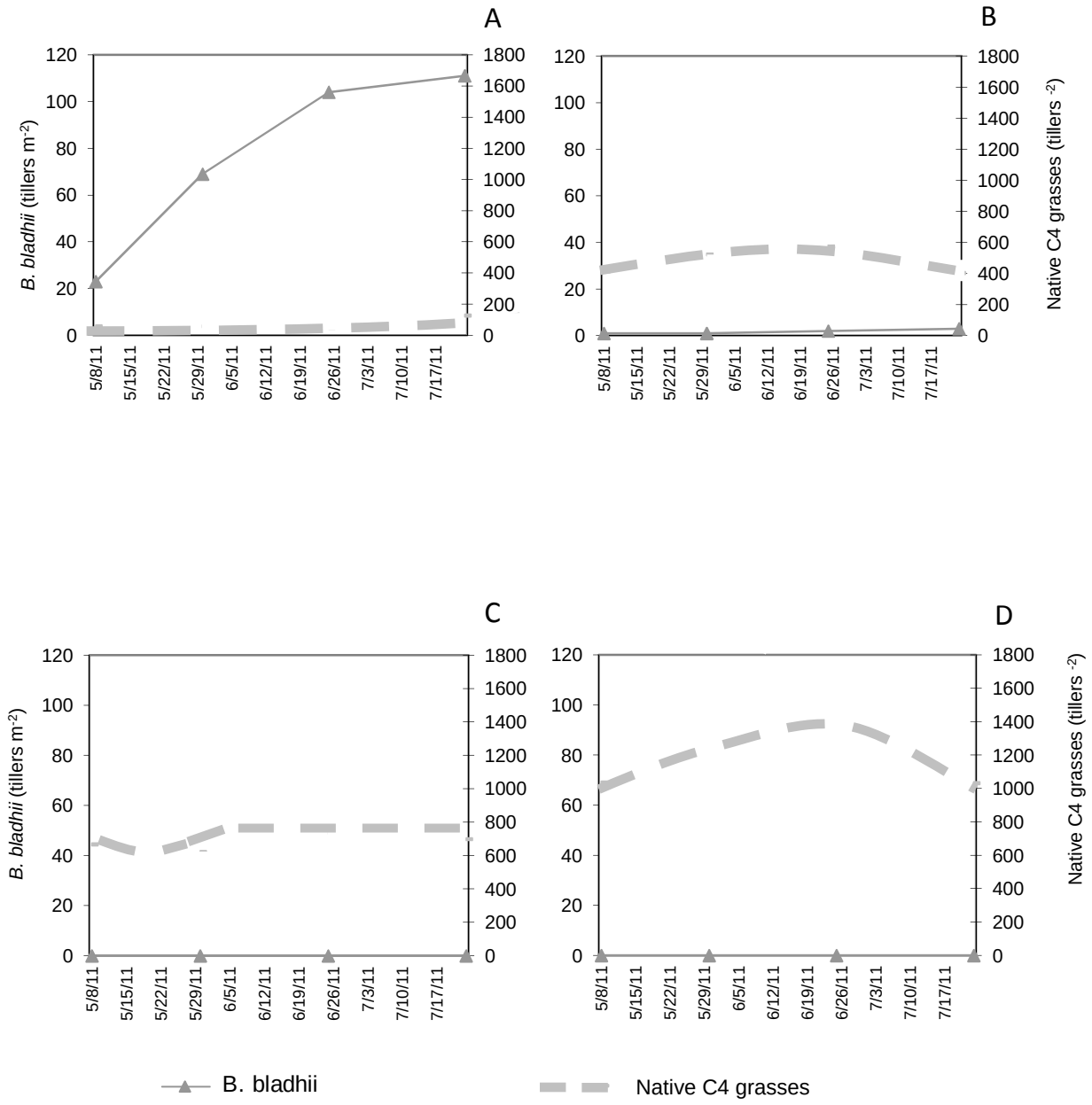
A
B
C
D
B. bladhii (tillers m-2)
Native C4 grasses (tillers -2)
0
20
40
60
80
100
120
0
200
400
600
800
1000
1200
1400
1600
1800
5/8/11
5/15/11
5/22/11
5/29/11
6/5/11
6/12/11
6/19/11
6/26/11
7/3/11
7/10/11
7/17/11
B. bladhii
Native C4 grasses

Figure 5.

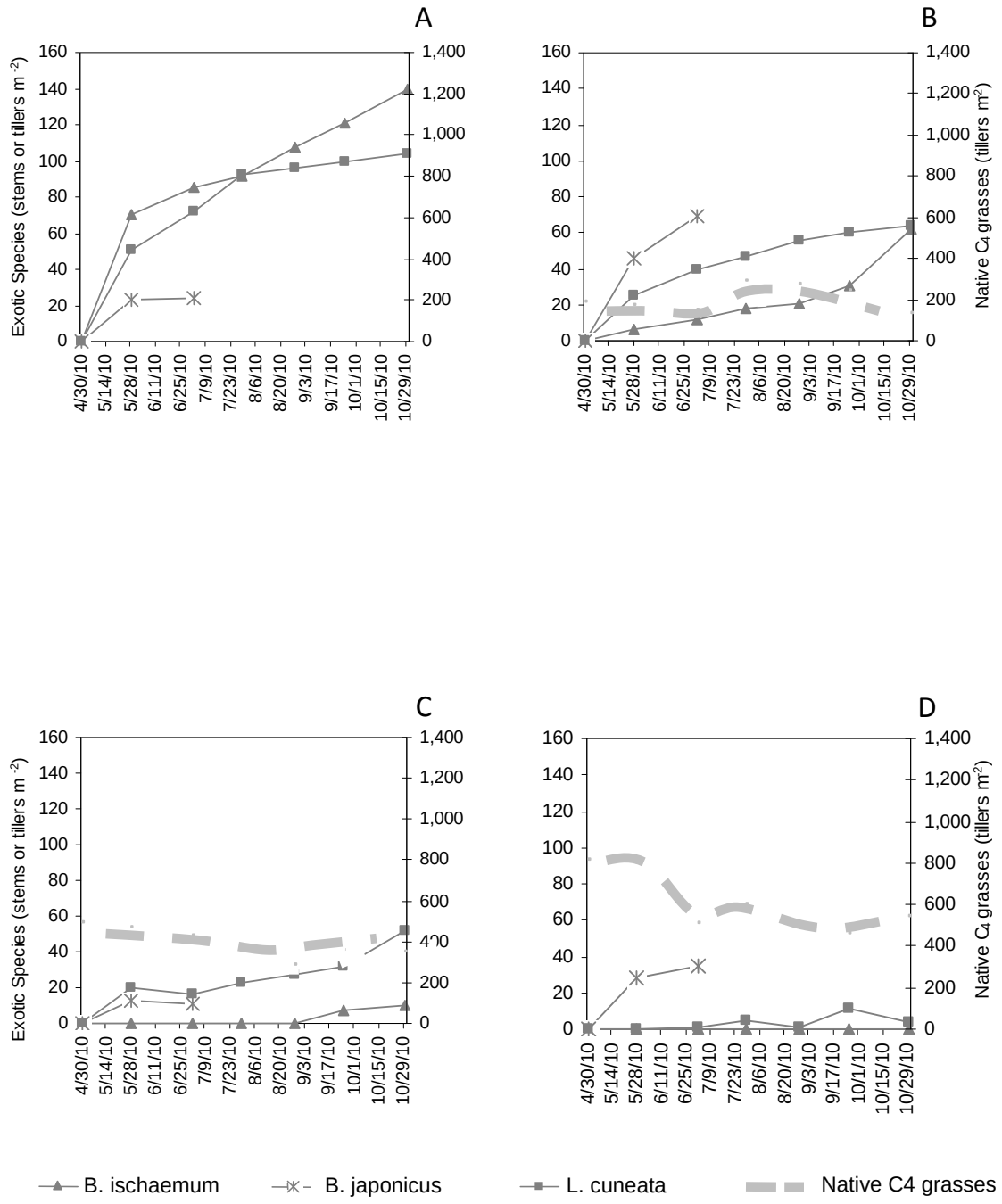
A
B
C
D
Exotic Species (stems or tillers m-2)
Native C4 grasses (tillers m2)
160
140
120
100
80
60
40
20
0
1,400
1,200
1,000
800
600
400
200
0
4/30/10
5/14/10
5/28/10
6/11/10
6/25/10
7/9/10
7/23/10
8/6/10
8/20/10
9/3/10
9/17/10
10/1/10
10/15/10
10/29/10
B. ischaemum
B. japonicus
L. cuneata
Native C4 grasses

Figure 6.

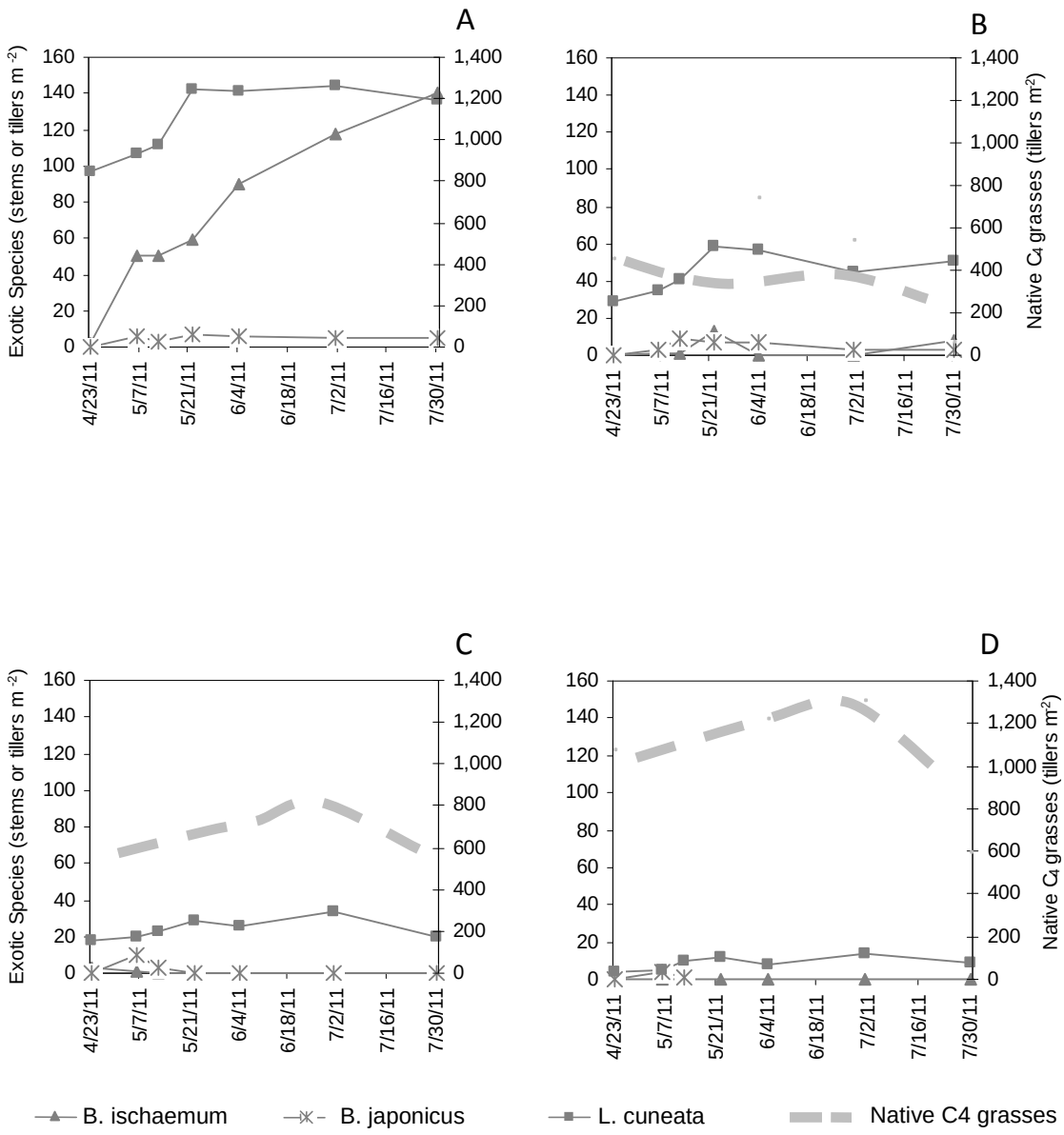
A
B
C
D
Exotic Species (stems or tillers m-2)
Native C4 grasses (tillers m-2)
160
140
120
100
80
60
40
20
0
1,400
1,200
1,000
800
600
400
200
0
4/23/11
5/7/11
5/21/11
6/4/11
6/18/11
7/2/11
7/16/11
7/30/11
B. ischaemum
B. japonicus
L. cuneata
Native C4 grasses

Figure 7.

FIGURE CAPTIONS

Figure 1. Hypothesized relationship between bud bank densities and native plant community invasibility and stability.

Figure 2. Two-year average bud:tiller ratio values at Konza Prairie Biological Station (A) and Oklahoma State University – Range Research Station (B), 2010 – 2011.

Figure 3. Konza Prairie Biological Research Station (A) and Oklahoma State University – Range Research Station (B) 2-year average invasive species production at 0%, 33%, 66%, and 100% native field bud densities, 2010 and 2011 growing seasons.

Figure 4. Oklahoma State University – Range Research Station exotic species (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) biomass at 0%, 33%, 66%, and 100% native field bud densities, 2010 (A) and 2011 (B).

Figure 5. Oklahoma State University – Range Research Station native warm-season (C4) grasses and exotic species (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) tiller and stem densities at 0% (A), 33% (B), 66% (C), and 100% native field bud densities, 2010.

Figure 6. Konza Prairie Biological Station native warm-season grasses (WSG) and exotic species (*Bothriochloa bladhii*) tiller densities at 0% (A), 33% (B), 66% (C), and 100% native bud bank densities, 2011.

Figure 7. Oklahoma State University – Range Research Station native warm-season grass and exotic species (*Bothriochloa ischaemum*, *Bromus japonicus*, and *Lespedeza cuneata*) tiller and stem densities at 0% (A), 33% (B), 66% (C), and 100% native field bud densities, 2011.

VITA

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